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FEMALE STERILITY IN POTATOES[1]

BY T. J. ARNASON[2]

Abstract

Between 600 and 900 ovules are estimated to begin development in single normal potato ovaries. The number of seeds per fruit ranged from 0 to 183 in 1941, from 7 to 472 in 1942.

Sectioned ovules from several potato varieties were examined. Estimates of the proportion of aborted ovules from freshly opened flowers or nearly mature buds were as follows: Minn. 75-5: 10%, Earlaine: 15%, Early Ohio: 20%, Irish Cobbler: 30-40%, Sebago: 60%, U.S.D.A. 46000: 80%, Netted Gem: 100%. Pollen from the first two varieties only in this list has been used successfully in crosses. In Netted Gem few gametophytes began development, most of the abortion occurring earlier. In the other varieties a larger proportion of the abortion became evident after gametophyte development had been initiated. In Sebago many embryo sacs were immature in freshly opened flowers. Inexact distribution of chromosomes at meiosis probably accounts for a part of the observed abortion. Sterility genes may be responsible for a part. Premature bud and flower abscission lowers the expressed fertility of all varieties but is more effective in some: e.g. Netted Gem and Early Ohio, than in others, e.g. Minn. 75-5 and Earlaine. Fertilization in Irish Cobbler occurred mainly two to four days after pollination; 50% of ovules in the upper half of the ovary showed endosperm divisions. Evidence of fertilization was seen in less than 5% of ovules of U.S.D.A. 46000 taken four days after pollination. Nutritive cells of the integument became considerably enlarged in many ovules containing aborted embryo sacs.

Introduction

The principal objects of the work reported in this paper were (1) to determine the approximate frequency of embryo sac abortion in some pollen-sterile varieties of potatoes, this to be compared with the frequency in male-fertile varieties; (2) to discover the stage or stages of development at which degeneration in ovules first becomes apparent; (3) to seek the causes of ovule failure.

Evidence is lacking that abortion is as common in potato ovules as in anthers. Many pollen-sterile varieties produce seed abundantly after the application of sound pollen to receptive stigmas. The abortion of pollen has been attributed mainly to previous meiotic failure (1, 2, 4, 5, 9). If irregular distribution of chromosomes occurs because of polyvalent configuration or because of incomplete correspondence of pairing chromosomes, similar irregularities might be expected in the meiotic divisions in ovules. If, however, the irregularities in anthers are wholly or in part attributable to

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more general physiological disturbance, e.g. poor food or water supply, growth hormone concentration, or temperature, the ovules might not be affected to the same extent.

Rees-Leonard (6) in a study of the Irish Cobbler variety found some evidence of degeneration at all stages of macrosporogenesis and embryo sac development. Some normal appearing, mature sacs were, however, also observed. Since this variety is a dependable seed producer when sound pollen is used, it is apparent that ovule abortion is not always extensive.

It was observed here that some of the pollen-sterile varieties could be induced to form seeds readily, while others very rarely produced seeds. A few (Netted Gem, Warba, some seedlings) have not produced any seeds although repeated pollinations have been made in each of several years. All of the investigated lines that produce considerable quantities of sound pollen are also good seed producers.

Materials and Methods

The investigation of ovule development has, so far, been limited to the varieties listed below.

(1) Netted Gem (Russet Burbank). Completely sterile.

(2) U.S.D.A. selection number 46000. Apparently this line is completely male-sterile. Seeds have been rarely obtained even after the use of sound pollen. The number of seeds in each ripened ovary has been small, usually under 20. However, in 1942 a fruit containing 137 seeds was obtained.

(3) U.S.D.A. selection 44488 (Sebago). It is even more difficult to obtain fruits from this variety than from U.S.D.A. 46000. In one year a few berries were obtained. Each of these fruits contained over 50 seeds.

(4) Irish Cobbler. The proportion of sound pollen grains is always rather small, usually under 30%. If good pollen is used seeds are readily obtained.

(5) Early Ohio. Because of early abscission of most of the buds few samples of pollen have been tested. Few sound appearing pollen grains have been seen. This variety may be classed as highly, perhaps completely, pollen-sterile. The few ripened fruits that were obtained had from 15 to 50 seeds each.

(6) U.S.D.A. selection 45075 (Earlaine). Pollen usually over 50% sound. This is a fairly dependable seed producer.

(7) Minn. selection 75-5. Sound pollen and viable seeds are produced in abundance by plants of this line.

The cytological material described in this paper was collected in the field, mostly in the period June 5 to July 15. The average daily temperature was usually between 60° F. and 70° F. and it was always below 75° F. for each of the three days immediately preceding collection.

For the investigation of ovule development buds of the same length were fixed together. The length from the base to the tip of the corolla was

measured. The buds or the pistils from the buds were immersed for a few seconds in acetic alcohol, the fixing being completed in Craf solution. Cross and longitudinal sections of ovaries were cut, mostly at 14 to 18 μ. Heidenhain's iron alum haemotoxylin seemed to be the most reliable of the stains tried for this material. Sections were mounted serially in Clarite.

Pistils were also fixed at various times after pollination to obtain data on the time of fertilization and the sequence of developmental changes after fertilization. An estimate of the proportion of fertilized and developing ovules in two varieties (Irish Cobbler and U.S.D.A. 46000) was made. In all plants heavy pollination was practised so that fertilization should not fail because of dearth of pollen.

Ovule and Seed Numbers

The number of ovules developing in a single ovary is probably somewhat variable between varieties, and, perhaps to a lesser extent, variable between ovaries of the same variety. The number is large and difficult to determine exactly. According to counts made by Dorothy Johnston* the number is between 600 to 900 in the varieties Minn. 75-5, Sebago, Irish Cobbler, and Netted Gem. Miss Johnston also counted the number of seeds in individual ripened fruits. The range, in 1941, was from 0 to 183.

That considerably larger numbers of seeds could be produced was shown in 1942. Seed counts from 117 fruits were made. The range was from seven in a small fruit to 472 in one of the largest.

The majority of berries collected in 1941 had from 20 to 100 seeds. In 1942 a considerable proportion of fruits had from 100 to 300 seeds. The largest number of seeds recorded following open pollination was 237 in a fruit of Minn. 75-5. Occasionally small seedless fruits have been observed on pollen-sterile plants, especially U.S.D.A. 46000.

The better fruit and seed production of the 1942 season is doubtless related to weather conditions, especially temperature. In the 1942 season cooler weather prevailed than in 1941. In July, which is a critical month for fruit production, the average temperature was above 70° F. for 18 days in 1941; for only one day in 1942.

Ovule Development Prior to Fertilization

Earlaine

Ovule development in the male- and female-fertile variety Earlaine will be described first, rather briefly.

Many ovule primordia were growing out from the placental surface in 3-mm. buds. The diameter of many of these primordia was about 60 μ. Archesporial cells were not distinguishable in the nucellus. In 4-mm. buds the integument was beginning to develop from the nucellus and in each ovule a single archesporial cell was enlarging to form the macrospore mother cell. First and

* *Research Assistant, 1941.*

second meiotic division figures were common in 5- and 6-mm. buds (Figs. 1 to 6). Spores (Fig. 7) were already present in many ovules; in some ovules the functional chalazal spore was considerably enlarged. A 7-mm. bud also yielded many ovules containing spores. The three spores which degenerate must, ordinarily, shrink and disappear rapidly since it is difficult to find them except when the second meiotic division is recently completed. The young functional spores enlarge rapidly; they are therefore variable in size. Commonly, those measured were about 12 μ wide, 15 to 20 μ long. At the four-spore stage two dimensions of the ovule were about $80 \times 120\ \mu$, exclusive of the short and somewhat variable stalk. At the time of the meiotic divisions, cell divisions were proceeding rapidly in all parts of the young integument. The integument was generally five or more cells in thickness at the chalazal end of the ovule at this time. The nucellus shrinks as the other parts of the ovule develop. Traces of the nucellus, often fragmentary, may be found, however, at least in the chalazal region, during all stages of embryo sac development.

The integument of ovules from 8- to 9-mm. buds was found to have increased to seven to nine cell layers. A common ovule size was $125 \times 180\ \mu$. Within single ovaries considerable variation in the development of the female gametophyte was observed, the range being from metaphase of the first meiotic division to the four-nucleate embryo sac. Of 138 ovules that were classified according to the developmental stages 115 were in the one- or two-nucleate gametophyte stage. A representative uninucleate sac was found to be 60 μ long, 24 μ wide at the widest point.

Many embryo sacs in 11-mm. buds contained only five distinct nuclei: the two synergid, single egg, and two polar nuclei. Like the aborting spores, so the three antipodal nuclei can, as a rule, be found easily just after they

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EXPLANATION OF FIGURES

All figures were drawn with the aid of a camera lucida, Figs. 2 to 5 inclusive, and Figs. 8 to 12 inclusive by Dorothy Johnston; all have been reduced one-half in reproduction.

FIGS. 1 TO 12. *Variety Earlaine. Fertile.*

FIG. 1. *M1 metaphase, polar; from 5-mm. bud. 1000×.*

FIG. 2. *M1 early anaphase, side view; from 7-mm. bud. 900×.*

FIG. 3. *M1 telophase, side view, nucellus and a portion of the integument shown; from 7-mm. bud. 500×.*

FIG. 4. *M1 telophase; from 7-mm. bud. 900×.*

FIG. 5. *M2 metaphase and late anaphase, some irregularity; from 5-mm. bud. 900×.*

FIG. 6. *M2 metaphases; from 5-mm. bud. 1000×.*

FIG. 7. *Linear row of four spores; from 7-mm. bud. 1000×.*

FIG. 8. *Telophase of first gametophyte division; from 8- to 9-mm. bud. 900×.*

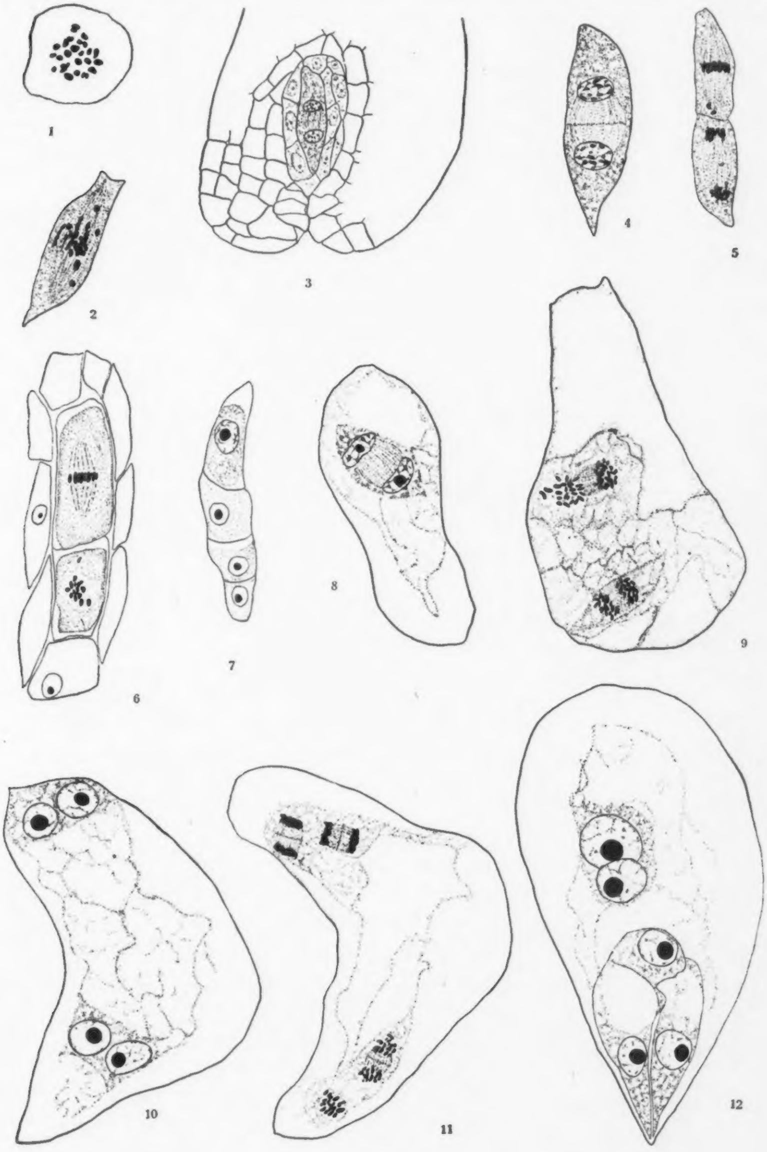
FIG. 9. *Anaphases of second gametophyte division; 24 chromosomes counted in one group; from 8- to 9-mm. bud. 900×.*

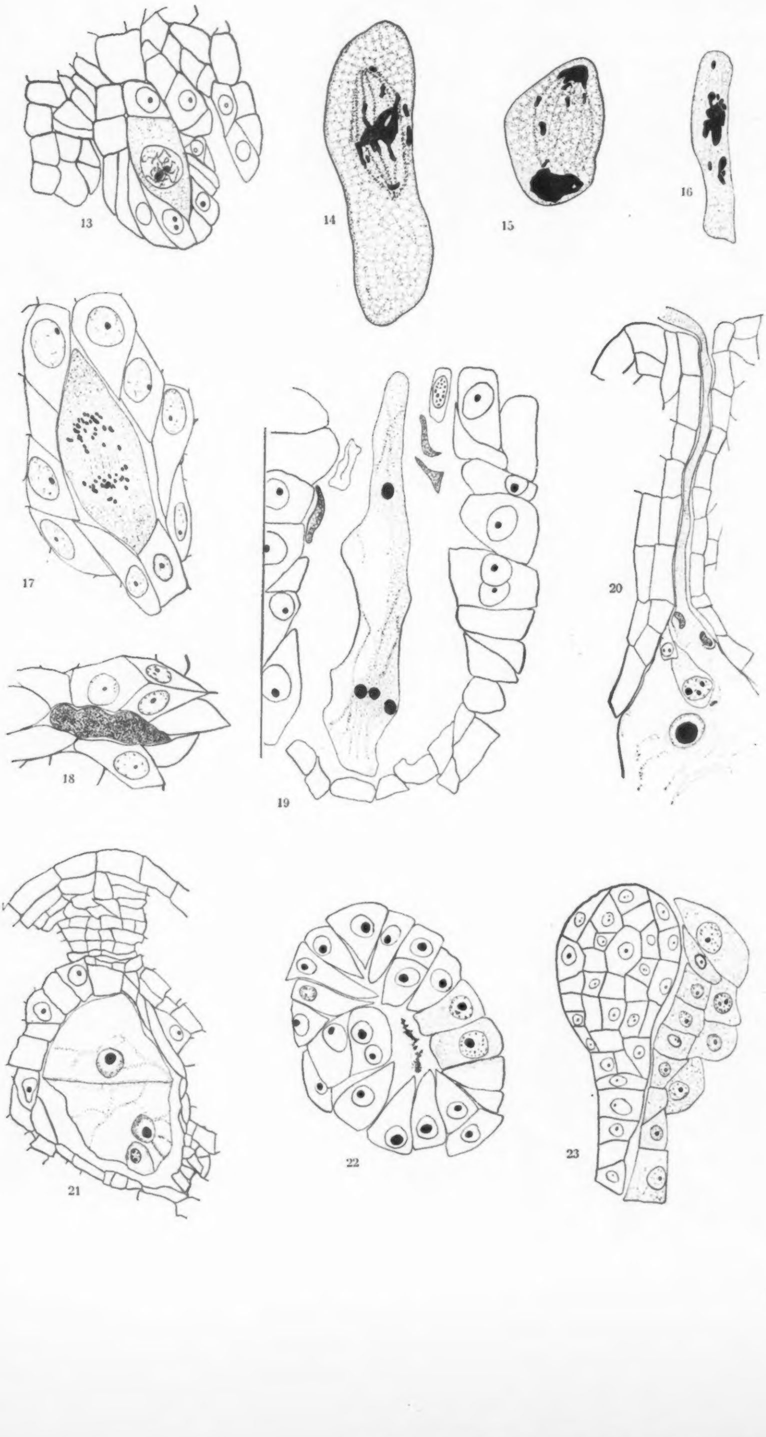
FIG. 10. *Four-nucleate gametophyte; from 11-mm. bud. 900×.*

FIG. 11. *Anaphase and early telophase stages of last gametophyte divisions; from 11-mm. bud. 900×.*

FIG. 12. *Nearly mature, four-celled, five-nucleate embryo sac; polar nuclei in contact; no trace of antipodals; from 14-mm. (ready to open) bud. 900×.*

are formed but not much later. In 25 out of 82 classified embryo sacs the last division had occurred. Most (48) of the remaining sacs were in the two- or four-nucleate stage (Figs. 8 and 10). Three second and three last game-

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tophyte divisions were found (Figs. 9 and 11). Typical ovule size at this time, i.e. as the gametophytes near maturity, was 150 × 190 μ. A nearly mature embryo sac was 78 μ long, 30 μ wide.

Most of the embryo sacs in buds that were about to open (about 14-mm.) were mature or nearly so. A few immature two-nucleate sacs were found, most of them near the base of the ovary. Roughly 25% of the sacs had two distinct polar nuclei; in slightly over 50% the two polar nuclei were in contact (Fig. 12) or fusing; in the remainder a single fusion nucleus was present.

Nearly median ovule sections commonly measured about 165 × 230 μ. In the late stages of ovule development integument cells enlarged considerably. Few division figures were found in integuments from 9- to 14-mm. buds. Next to the embryo sac (or nucellus, where present) was a single layer of large "nutritive cells" of the integument. The radial length of these cells was seldom over 10 μ, often it was considerably less.

Few aborting embryo sacs were found at any stage of development. Little irregularity was detected in the meiotic figures found; the irregularities consisted mainly of a few chromosomes slightly off the plate at metaphase of the first division, and a few chromosomes slightly apart from the main chromosome groups at first anaphase (Figs. 1 to 6). In a few two-nucleate and four-nucleate embryo sacs, the cytoplasm and nuclei were shrinking and becoming disorganized. When immature and obviously disorganized sacs of mature buds were lumped together, the total stood below 15%.

EXPLANATION OF FIGURES

All figures were drawn with the aid of a camera lucida, Figs. 14 and 15 by Margaret Wilson (Research Assistant, 1942); all have been reduced one-half in reproduction.

FIG. 13. *Early Ohio. Macrospore mother cell in early prophase stage; integument growing out from nucellus; from 4-mm. bud. 675×.*

FIG. 14. *Netted Gem. M1 metaphase, many chromosomes off the plate; from 6- to 7-mm. bud. 1500×.*

FIG. 15. *Netted Gem. M1 late anaphase, several chromosomes apart from main groups; from 6- to 7-mm. bud. 1500×.*

FIG. 16. *U.S.D.A. 46000. Dense central irregular chromosome mass, several chromosomes apart from main group; from 6- to 7-mm. bud. 1000×.*

FIG. 17. *U.S.D.A. 46000. M1 anaphase, two distinct but rather scattered groups of chromosomes; from 6- to 7-mm. bud. 1000×.*

FIG. 18. *U.S.D.A. 46000. Dense central lobed mass in ovule; early abortion, possibly at four-spore stage; from 7- to 9-mm. bud. 1000×.*

FIG. 19. *U.S.D.A. 46000. Aborting four-nucleate gametophyte, nuclei disintegrating, nucellar cells mostly shrivelled, portion of nutritive layer of integument shown, from 14-mm. (mature) bud. 1000×.*

FIG. 20. *Irish Cobbler. Pollen tube entering embryo sac from micropyle; fusion nucleus, egg cell, and one synergid visible in embryo sac; the dark bodies near the tip of the pollen tube are probably sperm nuclei; three days after application of Earlaine pollen. 540×.*

FIG. 21. *U.S.D.A. 46000. Unicellular zygote and two-celled endosperm; integument cell layers at chalazal end of embryo sac shown; four days after pollination by Minn. 75-5. 360×.*

FIG. 22. *U.S.D.A. 46000. Disorganized gametophyte surrounded by enlarged cells of the nutritive layer of the integument; four days after pollination by Minn. 75-5. 540×.*

FIG. 23. *Irish Cobbler. Embryo at "suspensor and ball" stage; a few endosperm cells (stippled) also shown; eight days after pollination by Minn. 75-5. 360×.*

Possibly over 85% of the ovules contained eggs capable of being fertilized. If there is a total of 700 ovules in each ovary one might expect to obtain about 600 seeds following heavy pollination. The number of seeds actually obtained from individual fruits has always been much less.

U.S.D.A. 46000

Ovules from 4-mm. buds of U.S.D.A. selection number 46000 were similar to those of Earlaine of corresponding size. In most ovules the macrospore mother cell was in an early prophase stage. Approximately 6% of the ovules had two macrospore mother cells instead of the usual one. Integument cells were actively dividing.

Prophases of the first meiotic division only were found in 5-mm. buds; the most advanced cells were at diakinesis. Metaphase and anaphase stages of the first division were seen in a few ovules from 5- to 6-mm. buds. Few irregularities were detected in these (early) division figures.

A considerable proportion of macrospore mother cells had advanced to metaphase and anaphases of the first division in 6- to 7-mm. buds (Figs. 16, 17). Approximately one-third of these figures were classed as irregular. In some of the metaphase figures the chromosomes, or groups of chromosomes, appeared to have coalesced; in some the only visible irregularity consisted of one or a few chromosomes off the plate. Similarly, the anaphase irregularities ranged from gross—two unequal chromosome masses with apparent fusion of chromosomes—to slight—single lagging chromosomes.

It does not seem probable that meiotic irregularities were caused by the pedicel abscission processes which in potatoes often cut off buds early. It was thought that as long as mitoses proceed actively in the integument the abscission mechanism is not interfering with ovule development. In all the buds (up to 9 mm.) numerous division figures were observed in the integument.

Macrospore mother cells are very slow in reaching late meiotic division stages in many ovules. In one 8-mm. bud the four spore stage had been reached in only 40% of the ovules. What the causes of the tardiness may be is undetermined. It is not known whether pairing difficulties in prophases might delay metaphase and succeeding stages.

A few ovules were seen in which the two daughter nuclei or daughter cells from the first division were degenerating. Three of the four spores normally degenerate. Occasionally the fourth (chalazal) spore also was seen to be breaking down.

Ovule counts were made from 9-mm. buds to determine the proportion having abortive gametophytes. From these counts it was estimated that not over 30% of the ovules had healthy spores or embryo sacs. The most advanced gametophytes were two-nucleate. Similar counts were also made in ovules of 11- and 12-mm. buds. Of 50 ovules 15 may have had functional embryo sacs. From what appeared to be a representative region in the ovary of a freshly opened flower, two out of 10 adjacent ovules had healthy

gametophytes. In a second ovary from an open flower only one out of 12 ovules had normal appearing egg apparatus and polar nuclei.

The aborting embryo sacs presented a variety of appearances (Figs. 18, 19, 22). Some were inflated but the nuclei showed signs of collapse or degeneration; some sacs were collapsed, appearing as a dense-staining narrow strand, with or without visible nuclei.

The nutritive cells of the integument were prominent in most ovules. As a rule these cells became enlarged in ovules having collapsed embryo sacs. In sections many of these cells were triangular, apices of many triangles converging in the central (embryo sac) region. The nutritive cells were even more conspicuous in older aborting ovules, collected a few days after pollination (Fig. 22).

From this investigation of ovule development it is concluded that there is considerable embryo sac abortion in this variety. Probably less than one-fifth of the ovules are functional at the time of pollination. Unequal or inexact distribution of chromosomes at meiosis is a probable cause of embryo sac abortion. The causes of the delayed and irregular meiotic division remain to be discovered.

Netted Gem

This variety has proved completely sterile. Microspore dyads were common in anthers. The pedicel abscission mechanism was relatively efficient, few open flowers being seen at any time. The majority of buds dropped off before reaching a length of 10 mm. Many of the (abscissing) buds sectioned had no division figures in the ovule integuments. The development of spores and gametophytes was studied as far as possible from healthy buds showing division figures in the ovule integument. In 5-mm. buds all stages from early prophases to anaphases of the first meiotic division could be found. The majority were in mid- to late prophases. Metaphases of the first division were fairly numerous also in the 6- to 7-mm. buds. Some of these were regular; some had one to many chromosomes off the plate (Fig. 14). The rather few anaphases observed were also variable. Several lagging chromosomes occurred in the cell drawn in Fig. 15.

The spore stage was already reached, and sometimes passed, in many ovules from 6- to 7-mm. buds. However, in a considerable proportion the macrospore mother cell or its derivatives appeared as one to four amorphous masses. It was difficult to judge the stage at which development had been arrested, probably, often, at a late stage of the first division. In a few ovules only one of the nuclei formed at the end of the first meiotic division divided; in these, three instead of four cells were present at the end of meiosis. Few second division figures and few spores of normal appearance were seen.

The only 8-mm. buds sectioned were some that were ready to drop, the abscission layer having cut through the pedicel. A few ovules had two- or four-nucleate sacs. In many ovules spores had enlarged to form game-

tophytes but most of these had been arrested in development before the second gametophyte division.

Sectioned buds 10 mm. long with pedicels still intact revealed that abortion was general prior to this stage. In two buds only four inflated and possibly healthy gametophytes were seen. Tapetum-like nutritive cells, greatly enlarged, occupied the central region of nearly every ovule. While the amount of material examined was not great, one may tentatively conclude that in the Netted Gem variety abortion in ovaries is complete or very nearly complete some time before flowers open.

The time at which development is arrested in most ovules has not been determined very exactly. It would be desirable to make a thorough study of young buds to find if the second meiotic division commonly occurs or not, and also to ascertain the commonness of such irregularities as lagging chromosomes, etc. at anaphases of the two meiotic divisions.

Pedicel abscission alone could account for much of the unfruitfulness of this variety, but the few flowers that open are believed to be sterile because of undeveloped or shrivelled gametophytes. Even in the absence of pedicel abscission complete female sterility would be expected.

U.S.D.A. 44488 (Sebago)

In spite of persistent application of pollen from many sources to stigmas of this variety fruits have been formed in only one year, and then only three or four. Pollen of this variety is mostly non-viable. It probably is unable to serve as pollen parent at any time.

A total of eight 4-mm. buds were examined. All were alike. Ovules were very young, archesporial cells being distinguishable in relatively few ovules. In 6-mm. buds a proportion, perhaps one-half, of the archesporial cells had begun early meiotic prophase stages. Very few had advanced to diakinesis. Two or three 8-mm. buds examined showed signs of general degeneration, probably from pedicel abscission. In the third bud, which appeared to be healthy, 16 out of 25 macrospore mother cells recorded were in pachytene stages or earlier, four were in diakinesis, three in metaphases, and two in telophases of the first division.

The slides were not searched for meiotic metaphases and anaphases. In the few metaphases seen all the chromosomes were closely aggregated on the plate.

Fairly general abortion was seen in 11-mm. buds. In many ovules a dense-staining strand consisting of one to four segments was visible. These probably were the degenerating products of the first or second division. A few ovules had somewhat expanded one- or two-nucleate gametophytes.

Pistils from buds that were about to open (14 mm.) had immature gametophytes in some ovules; in others, aborting sacs, spores, or prespore cells were visible but often not classifiable as to the stage at which development had ceased and disintegration had begun. These are included below in the class "aborted spores". Fifty-one ovules picked at random were classified

as to stage of development. Thirty-one were in "aborted spore" condition, no embryo sac enlargement having occurred; there were two one-nucleate sacs, in one of which the nucleus was dividing, eight two-nucleate, seven four-nucleate, and three immature eight-nucleate sacs.

In general this variety appears to be characterized by relatively very slow development of the gametophytes together with considerable (about 60% in the examined material) early abortion. It might be supposed that, in crossing, repeated pollination of the same flowers might result in a higher proportion of fertilized eggs than single heavy pollinations. The flowers that open tend to persist for several days.

Minn. 75-5

The ovules from 4- and 5-mm. buds of the highly fertile Minn. 75-5 line were well advanced. Pachytene to spore stages of the first division were most common. In one bud many of the functional spores had enlarged considerably. The chromosomes were compactly and smoothly arranged on most of the equatorial plates of the first division. A few irregular metaphases with a number of chromosomes scattered off the plate were observed.

In some first anaphase figures chains of chromosomes connected the two main groups. It became evident that irregularities in chromosome distribution occurred at meiosis in some cells. Three healthy 6-mm. buds were examined. All were similar, the observed range of gametophyte development being from spore to four-nucleate sac. Two-thirds of the ovules had two-nucleate sacs.

Several 8- to 11-mm. buds were examined. Two- and four-nucleate gametophytes were commonest; there were very few one-nucleate or eight-nucleate sacs. One exceptional 8-mm. bud had no stages beyond unexpanded spores.

In 12- to 13-mm. buds a sprinkling of eight-nucleate sacs was observed. Four-nucleate gametophytes were, however, most abundant.

The last gametophyte division had been completed in slightly over two-thirds of the ovules from 14-mm. buds. The remaining ovules had two- or four-nucleate gametophytes. Few definitely aborted embryo sacs were observed.

Irish Cobbler

The youngest buds examined were 6 mm. Spores and young gametophytes, one-, two-, and four-nucleate, occurred in the ovules. In 8- and 9-mm. buds, two-, four-, and eight-nucleate and nearly mature embryo sacs occurred. Twenty embryo sacs were picked at random, of these nine were two-nucleate, eight were four-nucleate, and three were eight-nucleate.

The last division was completed in most of the healthy embryo sacs of 11- and 12-mm. buds. Between 30 to 40% of ovules had aborted. In many aborting ovules, the gametophyte had grown considerably prior to deterioration; the spore stage was definitely passed.

Early Ohio

Almost every ovule in a 5-mm. bud examined had a one-nucleate embryo sac. The only other buds sectioned were 11 mm. and 14 mm. In both, sacs nearing maturity were most prevalent. In the 14-mm. bud it was estimated that over 80% of the ovules had mature or nearly mature healthy sacs.

Some loose buds (abscissing) were also sectioned. Of these the large ones (14 to 15 mm.) are perhaps of most interest. Many large clear sacs were evident, often with only one or two nuclei present. Some were four- and some five-nucleate. It was believed that in some of the sacs development had been arrested prior to, in others after the last gametophyte division. The polar nuclei appeared to be affected last, the cells of the egg apparatus shrinking and disintegrating earlier. The ovule cell layers lying next to the embryo sac were collapsed, flattened, and often apparently dead (no organized internal structure visible).

Postpollination Changes

Pistils of only two varieties, collected one to several days after pollination, have been examined.

Pollen tubes were only part way down the style in Irish Cobbler one day after pollination; after two days, some tubes had reached embryo sacs; in a few ovules the endosperm was two-celled. In pistils collected three days after pollination, large numbers of pollen tubes were seen entering the locules at the top; a number of tubes were seen in ovule micropyles (Fig. 20). Some cases of fertilization were observed and in several to many sacs the triploid endosperm nucleus was dividing, or the endosperm was already two- or four-celled. Clarke (3) reported fertilization in Earlaine 36 hr. after pollination. It is probable that in Irish Cobbler the majority of ovules were fertilized two to four days after pollination, though a few were undoubtedly fertilized within two days of pollination.

The number of integument cells was increasing rapidly in ovules taken three days after pollination. Embryo sacs and ovules were enlarging. In recently fertilized ovules in which the endosperm was one- to four-celled, embryo sacs were 49 to 60 μ wide, 90 to 110 μ long; ovules were about 200 μ wide by 275μ long; nutritive cells had not changed much from the earlier condition, the largest having a radial length of about 15 μ.

Material collected five days after pollination was used to determine the proportion of ovules continuing development after fertilization. In the upper and mid-part of one ovary counts of groups of ovules gave 18 developing (e.g. multicellular endosperm) and 18 unfertilized or not developing. In the lower part of the same ovary, seven ovules were developing, 66 were not. As might be expected, the relatively high pollen tube concentration in the top portions of the ovary results in a higher proportion of fertilized eggs than in the lower regions. In some sections at least one-half of the ovules were continuing development. This indicates also that the estimate of 60 to 70% of

fertile gametophytes in this variety, arrived at from examination of buds and young flowers, was probably nearly correct.

In the U.S.D.A. 46000 line few healthy embryo sacs were present in pistils collected three and four days after pollination. Of several hundred ovules examined only six embryo sacs were seen in which endosperm divisions had occurred. One of these is drawn in Fig. 20. Very few pollen tubes could be found in the ovary locules. The few that were seen were all at the top. It is therefore possible that pollen tubes grow slowly in the styles or locules of this variety.

In four-day-old material, an estimated 80% of ovules contained visibly aborted embryo sacs. This figure is similar to that arrived at from a study of late buds and fresh flowers.

The cells of the nutritive layer of the integument were greatly enlarged in many, but not all, aborting ovules. The enlarged tapetum-like cells occupied the central region, if embryo sacs were collapsed or undeveloped (Fig. 22). In places the width of the nutritive cell layer was 21 to 30 μ. Some of the cells were binucleate. Division figures in the integument were very rare in all ovules in contrast to the great cell activity in the integuments of Irish Cobbler ovules a similar length of time after pollination.

Very few embryos were found in an ovary fixed eight days after pollination. Fifteen ovules of one section were examined in detail. One of these had a unicellular zygote. The endosperm was approximately eight-celled. None of the others gave any evidence of having been fertilized. In five of them there was scarcely a vestige of the gametophyte visible. The remainder had small embryo sacs, usually with one or more nuclei, or remnants of nuclei in each one. In fertile varieties embryos are multicellullar, at or near the suspensor and ball stage (Fig. 23) eight days after pollination.

Discussion

The investigation of young ovules of several varieties of potatoes has revealed that in most of them a considerable proportion of ovules abort. Abortion may occur at, before, or after the spore stage. In the Netted Gem variety, very few ovules had enlarged spores or gametophytes; in other varieties a larger proportion of failures became evident after gametophyte development had been initiated.

In Table I the estimated proportion of sound pollen grains and sound embryo sacs of each variety is given. Soundness was judged from appearance under the microscope. Pollen (when available) was taken repeatedly for examination.

It is apparent from the table that there is generally a higher proportion of functional macrospores (if the three which normally abort in each ovule are disregarded) than of functional microspores. Except for the most fertile varieties, correspondence between macro- and microspores is not close. In a number of cases the proportion of functioning chalazal macrospores is over 30% higher than that of microspores of the same variety.

TABLE I

ESTIMATED PROPORTIONS OF SOUND POLLEN GRAINS AND SOUND EMBRYO SACS OF SOME POTATO VARIETIES

Variety or line	Sound pollen, % (1941 records)	Sound embryo sacs, %
Minn. 75-5	52.3–81.8	90
Earlaine	0.0–69.4	85
Irish Cobbler	9.1–37.6	60–70
Sebago	0.0– 7.4	40
U.S.D.A. 46000	0.0– 5.2	20
Early Ohio	No pollen	80
Netted Gem	No pollen	0.0

Because of the very large numbers of ovules in each ovary, and the fact that fruits can mature though only a few seeds are developing, there can be a high ovule abortion rate without female sterility becoming macroscopically evident. From the estimates made, assuming 600 ovules per ovary, the number of potentially functional ovules would be: Minn. 75-5: 540, Earlaine: 510, Early Ohio: 480, Irish Cobbler: 360+, Sebago: 240, U.S.D.A. 46000: 120, and Netted Gem: 0. It is of interest to notice that the varieties showing 60% or over of undeveloped or degenerating embryo sacs have proved refractory seed producers. Possibly the proportion of non-functional embryo sacs is higher than was evident from their appearance. Other possibilities are that pollen tube growth may be slow in the styles of these varieties, or the aborting ovules in the ovary locules may tend to check or inhibit pollen tubes there.

The prevalent pedicel abscission introduces a complicating factor. Abscission will of course stop development of all structures above the cut. Whether abortion in anthers or ovules is a factor in inducing premature abscission, is more difficult to answer. From the fact that in Early Ohio, relatively little embryo sac abortion was observed to occur, and that early pedicel abscission in that variety was the rule, few buds reaching the open flower stage, ovule fertility is judged to be ineffective, or largely so, in preventing abscission.

It is probable that irregularities in chromosome distribution at meiosis are responsible for some spore and gametophyte degeneration. The small size of the chromosomes and their large number makes it very difficult to determine exactly the pairing relations of chromosomes. Irregularities that can be detected most easily are chromosomes off the plate at metaphase or apart from the main groups at anaphases or telophases. Lagging and wandering chromosomes occurred in some cells of all varieties in anaphases of the first meiotic division. The greatest observed irregularity was in Netted Gem, but even the highly fertile Minn. 75-5 had some very irregular appearing first anaphase figures. A more thorough study of meiosis in a few selected varieties is planned. The possibility that meiotic irregularities are greater at high than at low temperatures should also be investigated further as Stow's (8) findings have not been confirmed.

Because of the very large number of ovules in each ovary, fertilization of all functional eggs probably occurs rarely even after heavy pollination. Pollen tubes probably fail to reach, or penetrate, some ovules. Since the ovules do not all mature at the same time, male gametes may not be available for all embryo sacs during their "receptive" period, at least if there is only one pollination. How long after attaining maturity embryo sacs remain functional is not known. If the period is short, slow-growing pollen tubes—as possibly in styles of U.S.D.A. 46000—may reach most ovules too late, thus increasing the apparent female sterility.

For undisturbed meiosis any chromosome having more or less than one homologue in the same cell has too many or too few. If too many the excess homologues tend to interfere with normal pairing and segregation. If potatoes are tetraploids, each chromosome may have three homologues. Whatever pairing and segregation difficulties might result from such a condition should be the same or very similar in anthers and ovules of the same variety. The proportion of micro- and macrospores aborting for this reason should be similar. But in some potato varieties microspore abortion is commonly near 100%, chalazal macrospore abortion less than 60%. Therefore, it seems unfair to charge all the pollen sterility to excess homologues.

That meiotic failure in anthers is genic rather than chromosomal is suggested by differences between varieties all of which have the same chromosome number ($2n = 48$) and all of which may be presumed to have similar chromosome sets. Observations made on the macrosporocyte divisions and on subsequent embryo sac development suggest that, in some varieties at least, meiotic failure is less conspicuous in ovules than in anthers.

A gene or set of genes that delays the second meiotic division might have quite different effects on macro- and microsporocyte divisions. At the end of the first division in anthers the two nuclei are not separated by a membrane, in ovules the nuclei are so separated. Some of the meiotic failure in microsporocytes has been attributed (1) to the interphase nuclei of the first division approaching each other, then failing to divide independently at the second meiotic division; this result could not occur in ovules provided a cell plate or membrane is formed prior to the second division.

Varietal, hence genic, differences exist also with respect to pedicel abscission. It is possible that some irregularities in development of sporocytes and spores are consequences of incipient or partial pedicel abscission.

The observed abortion of ovules may be, in part, a result of the action of more or less specific lethal or semilethal genes acting on macrospores or gametophytes. If there are such genes, they may also cause pollen sterility since, as far as the writer is aware, no variety with high pollen fertility is female-sterile.

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EFFECT OF STORAGE ON THIAMIN CONTENT AND ON DEVELOPMENT OF RANCIDITY IN WHEAT GERM[1]

By J. A. Pearce[2]

Abstract

Wheat germ samples with moisture content varying between 8.0 and 26.5% were stored in air in sealed tins at −40.0°, −26.1°, −17.8°, −9.4°, −1.1°, 15.6°, and 23.9° C. The appearance of organoleptic spoilage appeared to be coincident with the termination of the induction period in oxidative rancidity development, as assessed by the peroxide oxygen value of the extracted oil. Storage life was considerably extended by holding at low moisture levels and low storage temperatures. However, even at −40° C. sufficient deterioration occurred to reduce the keeping quality of wheat germ subsequently stored at higher temperatures. Both packing in nitrogen and compressing into blocks lengthened storage life. Thiamin content, determined by the method described, did not change during storage.

Wheat germ oil expressed by pressure became rancid more rapidly than oil extracted with petrol ether. Increase in temperature markedly decreased the storage life of the oil.

Present indications are that protein hydrolysis may be a more important factor than fat spoilage in the deterioration of wheat germ.

Introduction

The present work was undertaken primarily to determine the storage life of wheat germ of various moisture contents, under a number of temperature and packaging conditions. It has been generally observed that wheat germ held under ordinary temperatures develops off-odours and flavours. However, there is little evidence to indicate whether the onset of these off-odours and flavours is associated with oxidation of the unsaturated fatty acids present. Some attempt was made, therefore, to determine the nature of the changes responsible for spoilage in wheat germ. Observations were also made on the thiamin content since this nutritionally important constituent may undergo oxidative decomposition. In addition, some data were obtained on the development of oxidative rancidity in stored oil expressed or extracted from wheat germ.

A number of changes have been observed in the chemical characteristics of stored wheat oils. During two months' storage at room temperature the Reichert-Meissl number and Kirschner number increased (4); during two and a half months' storage the iodine number increased slightly, but the acid number increased two to sixfold (5).

The change in acidity of wheat germ during storage has also been measured (13). The daily rate of increase in acidity varied with the temperature of storage, and at 29° C. was eight to 10 times greater than at −10° C.

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Methods

Moisture Content

Moisture content was determined by the official vacuum oven method for cereal foods (1, p. 211).

Peroxide Oxygen

The peroxide oxygen determination was selected for use in this study, since it was found to be a convenient measure of oxidative rancidity in fats and correlates highly with other rancidity measurements (14). The method used was a modification of the iodimetric procedure for determining peroxides in fats (2). Peroxide oxygen values are recorded as ml. of 0.002 *N* thiosulphate per gram of extracted oil. The method of extracting the oil prior to analysis has been described (14).

Thiamin

Three extraction methods were tested; the results are shown in Table I. The simple acid extraction (12) was much faster than the complete, modified Pyke extraction (8) or the pepsin digestion alone. A possibility that alkali may destroy part of the thiamin was noted (15, pp. 158-165); therefore the alkaline takadiastase step in the modified Pyke method was omitted, pepsin digestion alone constituting the third extraction method. As shown in Table I, the complete modified Pyke extraction produced comparatively low results. The simple acid extraction method was chosen for the present work.

TABLE I

COMPARISON OF THREE METHODS OF EXTRACTING THIAMIN FROM WHEAT GERM, MEANS OF SIX DETERMINATIONS

Sample No.	Acid extraction, γ/gm.	Modified Pyke extraction, γ/gm.	Pepsin digestion, γ/gm.
1	15.7	14.7	15.5
2	15.4	15.1	15.6
3	16.0	14.2	15.2
4	15.8	15.4	15.8
5	15.2	15.1	15.7
6	15.4	15.4	15.2
Average	15.6	15.0	15.5

Analysis of variance

Variance attributable to:	Degrees of freedom	Mean square
Extraction method	2	3.979*
Residual error	15	0.710
Error within extractions	90	0.125

* *Exceeds 5% level of statistical significance.*

Details of the acid extraction method as applied to wheat flour have been published (12), and the method was applied to wheat germ with the following modifications: a 3-gm. sample of wheat germ was extracted with 50 ml. of 1% hydrochloric acid, the supernatant liquid removed, the residue washed with 50 ml. of distilled water and centrifuged, the combined extract and wash water made up to 250 ml., and 3 ml. taken for oxidation to thiochrome. The aliquot of extract was oxidized by the addition of 1 ml. of 40% sodium hydroxide and an appropriate quantity of 0.1% potassium ferricyanide. The mixture was made up to 10 ml. with distilled water, and 15 ml. of isobutanol added. Other details were identical with those of the method for wheat flour. The photofluorometer used (16) was calibrated with solutions obtained by oxidizing thiamin hydrochloride solutions of known concentration.

Certain observations were made regarding application of the method to wheat germ. Complete extraction of thiamin was verified by analysis of a second wash with 50 ml. of water, in which no detectable thiamin was found. It was observed that too large or too small a quantity of potassium ferricyanide may affect the results adversely (Table II). The optimum quantity was readily determined by adding ferricyanide solution dropwise until the mixture was faintly yellow. Results were decreased about 20% if the order of addition of reagents was reversed, i.e., if potassium ferricyanide solution was added prior to the addition of sodium hydroxide. The recommended use of methyl alcohol during the oxidation procedure (11) was found to be superfluous in the analysis of wheat germ, as average values obtained with and without methyl alcohol were 14.3 and 14.2 γ/gm. respectively. The suggested use of 30% hydrogen peroxide (8) was also found to be unnecessary, as average values with and without peroxide were 15.7 and 15.6 γ/gm.

TABLE II

THE AMOUNT OF POTASSIUM FERRICYANIDE (AS ML. 0.1% SOLUTION) REQUIRED FOR MAXIMUM OXIDATION OF THIAMIN TO THIOCHROME IN WHEAT GERM

$K_3Fe(CN)_6$, ml.	Thiamin, γ/gm.	$K_3Fe(CN)_6$, ml.	Thiamin, γ/gm.
8.0	10.8	1.0	15.0
6.0	12.9	0.5	14.7
4.0	14.9	0.25	10.4
2.0	14.9		

Material and Procedure

A study was made of the effects of storage time and temperature on wheat germ[1] of normal moisture content (12.5%), stored under air in sealed tins. The storage temperatures used were −40.0°, −26.1°, −17.8°, −9.4°, −1.1°, 15.6°, and 23.9° C., i.e. −40°, −15°, 0°, 15°, 30°, 60°, and 75° F. Temperatures were maintained within ± 1.7° C. (± 3.0° F.).

[1] *Wheat germ used in this study was kindly supplied by Maple Leaf Milling Company, Port Colborne, Ont.*

For many food materials, moisture content is an important factor in determining storage life. Therefore, storage studies were made on wheat germ with moisture content altered by vacuum drying or exposure to saturated air for short periods at room temperature. Moisture content varied between 8.0 and 26.5%. Water was sprayed directly into wheat germ and the material thoroughly mixed to obtain the highest moisture content of 26.5%.

Preliminary evidence indicated that wheat germ held at low temperatures deteriorated to an extent that affected subsequent study at higher temperatures. This point was examined by storing a portion of the material at −40° C. for three months prior to storage at higher temperatures.

Two additional methods of packaging were investigated, namely, storage in an inert atmosphere and compression into cakes. An inert atmosphere was provided by filling the tins with nitrogen. The tins were evacuated three times through a small opening, the vacuum broken each time with nitrogen bubbled through pyrogallol, and the opening quickly soldered after the last filling. Material pressed into cakes was subjected to a pressure of 2.5 tons per square inch for 30 min. at room temperature. Even this treatment failed to form a block that retained its shape: the compressed blocks were stored, but had fallen apart at the end of two weeks' storage. During compression a small part of the oil was expressed; this oil was stored in glass phials sealed with paraffin wax, for comparison with oil extracted by petrol ether and stored under the same conditions.

Results

Peroxide Oxygen Value and Off-odours

To ascertain the relation between the peroxide oxygen value and spoilage detectable by organoleptic methods, 10 duplicate samples of wheat germ were tested. Five samples showed different peroxide oxygen levels; at the time, no peroxide oxygen was detected in the other five samples but measurable values were observed at different later dates. Six people were requested to smell and arrange each of the duplicate groups of 10 samples in the order of rancidity.

The results of the organoleptic test were divided into two groups for statistical treatment. Group I consisted of the five samples showing different peroxide oxygen values and Group II consisted of the five samples showing zero peroxide oxygen but arranged in the order of subsequent appearance of this value. It is evident from Table III that the organoleptic test did not detect significant differences between the individual samples over the entire experiment. However, comparison of the mean values showed that the group of samples without peroxide oxygen were preferable to the group with detectable peroxide oxygen. This preference was highly significant statistically indicating coincidence between the termination of the induction period of oxidative rancidity and the appearance of some form of spoilage detectable by organoleptic methods. The difference in the duplicate error for the two

TABLE III

RESULTS OF ODOUR TEST ON WHEAT GERM

Group	Sample	Peroxide oxygen value[1]	Mean score[2]
I	1	2.23	−1.12
	2	1.35	−0.36
	3	1.02	−0.41
	4	0.87	−0.33
	5	0.65	−0.95
II	6	0	0.66
	7	0	0.46
	8	0	0.46
	9	0	0.89
	10	0	0.69

Analysis of variance

Variance attributable to:	D.f.	Mean square	
		Group I	Group II
Samples	4	1.6593	0.3854
Individuals	5	0.1596	0.1596
Individuals × samples	20	0.6441	0.3976
Duplicate error	30	0.2251	0.5157

[1] *As ml. 0.002 N thiosulphate per gram extracted oil.*
[2] *Mean of scores applied to ranked data.*

groups may indicate that individual judgment may be better if some form of rancidity is present.

Peroxide Oxygen Development During Storage

Since a relatively small peroxide oxygen value is indicative of the presence of some form of rancidity, the data in Table IV were arranged to show the number of weeks' storage required for the development of a 1-ml. peroxide oxygen value.

Oil extracted from these storage samples was of such a nature that the use of the peroxide oxygen determination could be applied with but mediocre success. In some instances small, isolated peroxide oxygen values were observed several weeks before regular increases commenced. The regular increases continued until the maximum of about 5 ml. 0.002 *N* thiosulphate per gram of extracted oil was reached, whereupon the value subsequently decreased to zero. In some cases, a second maximum developed later in the storage period.

It is apparent that decreased moisture content appreciably retarded the onset of oxidative rancidity during the storage of wheat germ (Table IV). The material mixed with water (moisture content of 26.5%) reached its

TABLE IV

THE EFFECT OF TEMPERATURE, MOISTURE CONTENT, PREVIOUS HISTORY, AND METHOD OF PACKAGING ON THE STORAGE LIFE OF WHEAT GERM

Temperature, °C.	Moisture content, %							
	14.8	12.5	10.1	8.0	13.3[1]	12.5	13.6	12.1
	Fresh wheat germ						Old wheat germ[2]	
	Packed in air					Packed in N_2	Packed in air	
	Storage time[3]							
23.9	1	7	13	15	12	16	1	2
15.6	1	6	13	15	12	15	1	2
− 1.1	3	14	15	17	15	16	2	5
− 9.4		15				17		
−17.8		16						
−26.1		17						
−40.0		18						

[1] *Pressed into cakes before packing.*
[2] *Wheat germ held at −40° C. for three months prior to storage at temperatures noted.*
[3] *Time in weeks to develop a peroxide oxygen value of 1 ml. 0.002 N thiosulphate per gram extracted oil.*

maximum peroxide oxygen value before it could be packed and only the decrease could be observed during storage. This material developed a very bad odour and considerable gas was evolved after three days' storage at 15.6° and 23.9° C. These results indicate that a study of germ stored at reduced moisture contents might yield valuable information.

Wheat germ stored at temperatures above −1.1° C. deteriorated very rapidly. Temperatures lower than −1.1° C., however, had no pronounced additional effect on storage life. Wheat germ stored for even a relatively short time at −40° C. suffered changes that seriously impaired its keeping quality.

Packing wheat germ in an inert atmosphere or after pressing into cakes increased the storage life markedly at the higher temperatures, but only slightly at −1.1° and −9.4° C. Leakage during storage may have been responsible for this behaviour (Table V).

The results of the study on wheat germ oil are given in Table VI. Here, the peroxide oxygen determination could be applied with more success. The maximum peroxide oxygen value was much greater than for stored wheat germ. Rancid odours were not noticeable in the oil until after the maximum peroxide oxygen value had been reached. Increase in temperature considerably shortened the storage life of the oil. At −17.8° C. the regular increase in peroxide oxygen had not commenced even after one year in storage. Wheat germ oil extracted with petrol ether kept better at 23.9° C. than oil obtained by pressure.

TABLE V

GAS COMPOSITION OF TINS OF WHEAT GERM PACKED IN NITROGEN (AFTER 16 MONTHS' STORAGE AT VARIOUS TEMPERATURES)

Storage temperature, ° C.	Gas composition (%) (averages of 5 tins)		
	Carbon dioxide	Oxygen	Nitrogen
23.9	14.8	0.4	84.6
15.6	6.6	4.2	89.2
− 1.1	1.1	16.1	82.9
− 9.4	0.4	19.8	79.8

TABLE VI

DEVELOPMENT OF PEROXIDE OXYGEN VALUES IN OIL, EXTRACTED FROM WHEAT GERM BY PRESSURE AND WITH PETROL ETHER, STORED AT DIFFERENT TEMPERATURES

Storage time, wk.	Temperature, ° C.				
	23.9	23.9	15.6	−1.1	−17.8
	Pressure extraction	Petrol ether extraction			
	Peroxide oxygen value[1]				
0	0	0	0	0	0
1	14.9	1.0	1.0		
2	14.8	2.0	1.1	0	0
3	24.9	3.6	2.0	0	
4		5.8	3.6	0.6	0
5	20.4	4.6	2.4	0	2.4
6	17.9	18.8	8.4	2.3	1.8
7		28.3	8.5	0	0
8	12.6	9.1	17.8	1.9	1.5
9		4.7	19.5	1.4	0
10	18.3[2]		20.9	0.1	0
12			11.4	2.6	0
15				0	0
20				9.1	0
25				12.7	5.6
30				7.8	1.6
35				8.8	1.8
40				9.3	0
45				29.7	0
50				24.8	0

[1] *As ml. 0.002 N thiosulphate per gram extracted oil.*
[2] *Mouldy sample.*

Change in Thiamin Content During Storage

Table VII shows the change in thiamin content of wheat germ during six months' storage at 15.6° C. The values observed here for the thiamin content of wheat germ compare favourably with some of the values in the literature (3, 6, 7) but are lower than a recently recorded value of about

TABLE VII

CHANGE IN THIAMIN CONTENT OF WHEAT GERM STORED AT 15.6° C.

Storage time, wk.	Thiamin content, γ/gm.	Storage time, wk.	Thiamin content, γ/gm.
0	14.2	9	15.2
2	15.5	10	15.0
6	15.2	17	15.4
7	15.8	26	15.3
8	15.3		

10 I.U. per gram (8). It is evident that wheat germ became inedible owing to spoilage without any detectable loss of thiamin content.

Discussion

The results seem to indicate that protein may be chiefly responsible for spoilage in wheat germ. It would be expected that rancidity in the oil would be due to the presence of decomposition products of the peroxide form of the fatty acids. The occurrence of detectable rancidity in the oil after maximum peroxide oxygen values were observed rather than with the commencement of measurable peroxide, as for the whole germ, is strong evidence for minimizing any influence the decomposed oil might have on the off-odours developed during wheat germ spoilage.

Some contradication of the above might be observed in a comparison of the maximum peroxide oxygen values occurring in the oil extracted from stored wheat germ with values for the stored oil. A more rapid breakdown of the peroxide form of the fat in the whole germ is indicated. This would have to be explained on some basis, such as the presence of a pro- or antioxidant insoluble in petrol ether; the antioxidant affecting the formation and the pro-oxidant affecting the decomposition of the peroxide form of the fatty acid.

In connection with the occurrence of small peroxide oxygen values before the regular increase to the first maximum, and the double maximum observed in oil extracted from stored wheat germ, it may be noted that the onset of measurable peroxide oxygen in the expressed oil occurred immediately as compared with the delayed development in the compressed material. It is possible that oxidation in the surface oil is completed before the remainder is attacked. Consideration must also be given to possible differential rates of decomposition of the peroxide form of fatty acids with one or two double bonds.

Methods of detecting protein decomposition were believed desirable, since protein was believed to be the chief factor responsible for wheat germ spoilage. When wheat germ was treated with 95% ethanol, a compound containing sulphur was evolved which produced stains on lead acetate paper. The possibility that the intensity of stain might be related to storage life

was investigated, but was found to be unsatisfactory. However, it was observed that the fluorescence (measured on a Coleman photofluorometer) of an extract of defatted wheat germ in 10% potassium chloride solution did reflect storage conditions (Table VIII).

TABLE VIII

FLUORESCENCE OF 10% POTASSIUM CHLORIDE EXTRACT OF DEFATTED WHEAT GERM

Condition of wheat germ	Fluorescence reading, photoflorometer units
Fresh	11.0
Stored six months at −40.0° C.	11.6
Stored six months at −17.8° C.	11.8
Stored six months at − 9.4° C.	12.4
Stored six months at − 1.1° C.	12.2
Stored six months at 15.6° C.	14.0

A more pressing need of objective tests as a measure of quality in dried whole egg powder (10) prevented a complete investigation of the application of the fluorescence test to wheat germ. Continued work on egg powder has indicated that proteins and products of protein hydrolysis are the fluorescing substances (9). This, when combined with the observation that reduced moisture content increased storage life, indicates that protein hydrolysis may be the major factor causing spoilage in wheat germ.

Since spoilage in wheat germ and dried whole egg powder seems to be similar in many respects, completion of the present investigations on dried eggs may be of material assistance in further work on wheat germ storage.

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L'ÉRABLIÈRE LAURENTIENNE

I. VALEUR D'INDICE DES ESPÈCES[1]

PAR PIERRE DANSEREAU[2]

Sommaire

L'aire de l'érablière est plus réduite que celle de l'espèce dominante (*Acer saccharophorum*): elle couvre toute la partie nord de la formation des bois feuillus qui s'étend entre les prairies et l'Atlantique et la forêt sclérophylle méridionale et la forêt coniférienne canadienne.

Cent quatre-vingts relevés ont été faits dans cette région d'après la méthode phytosociologique de Braun-Blanquet. Les sites ont été choisis au hasard afin de ne préjuger en rien de la composition ou de la physionomie de l'érablière type.

Chacune des 346 espèces relevées au moins une fois a été soumise à un examen afin de déterminer sa valeur écologique. Il s'agissait de la classer par rapport à cinq facteurs: forme biologique, réaction à la lumière et à l'humidité, fidélité relative à l'érablière, et pourcentage de présence dans les 180 relevés. Les tableaux, réduisant ces données à une formule simple, établissent le status écologique de chaque espèce.

A ces formules sont attribuées des valeurs qui correspondent à la puissance constructive ou destructive de l'espèce par rapport à l'érablière. Ces valeurs sont les indices qui à leur tour nous permettront d'établir l'indice floristique-moyen de chaque érablière, en tenant compte de l'abondance et du nombre des espèces.

Aire de l'érablière

Une ceinture de bois décidus mésophiles s'étend sur une portion importante de l'Amérique du nord-est, limitée à l'ouest par la steppe (grassland), au nord par la forêt canadienne[3], et au sud par des forêts sclérophylles (Fig. 6). Cette formation relativement homogène se subdivise en régions dont chacune offre un facies particulier selon les conditions dues à la latitude, à l'humidité, et à la chaleur: chênaies et érablières surtout.

Dans la région laurentienne, les bois décidus de première venue sont représentés par l'érablière (Fig. 1E). Il est, en effet, encore douteux qu'il existe à proprement parler des chênaies (Fig. 1Q), et celles-ci font plutôt figure de reliques (Mont-Royal) ou de pionnières (vallée de l'Ottawa). Nous entendons ici par région laurentienne non pas tout le bassin du Saint-Laurent, mais plutôt son cours moyen: soit, au nord: des environs de la ville de Québec jusqu'à la frontière ontarienne et sur une largeur variant entre trente et cent milles au nord dans les Laurentides, et depuis Montmagny au sud, tout le triangle compris entre le fleuve et la frontière américaine (voir Fig. 6 zone indiquée par les lignes brisées).

[1] *Manuscrit reçu le 30 juillet 1942.*

[2] *Chargé de cours à l'Institut de Biologie de l'Université de Montréal, Montréal, Qué., et à Macdonald College (McGill), Macdonald College P.O., Qué.*

[3] *L'expression "forêt canadienne", déjà consacrée par plusieurs auteurs, sera employée constamment ici de préférence a "forêt coniférienne" pour désigner la formation septentrionale dominée par les épinettes et le sapin (Picea et Abies). Les bois de pin blanc (Pinus strobus) et de pruche (Tsuga canadensis) ont une distribution et un status écologiques très différents de ceux de la forêt canadienne.*

Certes, les bois où domine l'érable à sucre ne s'arrêtent pas à ces limites puisqu'on en trouve des étendues considérables dans les Etats-Unis du nord jusqu'au Wisconsin à l'ouest, et jusqu'au Maryland au sud, et dans l'Ontario au nord-ouest. Soit à peu près ce que Weaver et Clements (16) ont appelé "Lake Forest". Or, la région considérée ici se trouve tout entière dans la zone de rusticité III telle qu'établie par Rehder (11), c'est-à-dire dans la zone où le minimum annuel moyen de température oscille entre 20° et 35° F. La frontière sud de cette zone divise donc à peu près en deux le domaine de l'érablière. De sorte que la région étudiée ici comprend le quart nord-est de l'aire générale et se trouve en contact avec une flore boréale et atlantique, alors que l'autre quart (nord-ouest) serait soumis à une influence boréale et continentale; tandis que la moitié sud serait en contact respectivement avec la chênaie et la flore appalachienne à l'est, et la chênaie et la flore continentale à l'ouest.

Cette même frontière, prise ici empiriquement comme limite, correspond cependant aux bornes assignées par plusieurs phytogéographes éminents (13, 14) à la forêt canadienne. Frère Marie-Victorin en fait la "région des bois feuillus tolérants". D'autre part, certains facteurs physiques font ressortir l'homogénéité de cette région, dont voici la description plus précise: (1) elle est comprise entre les 45° et 47° de latitude nord et les 71° et 76° de longitude ouest; (2) les précipitations sont de 40 à 60 pouces par année; (3) l'écart moyen de température est de 32° F.; (4) les isothermes de janvier sont de 8° F. au nord et de 16° F. au sud, ceux de juillet, respectivement de 64° F. et de 72° F. (7). La position précise des lignes isothermiques suffirait à nous convaincre de l'homogénéité de l'aire en question au point de vue climatique. La plupart des cartes phytogéographiques le confirment d'ailleurs en indiquant une compénétration assez forte de la forêt canadienne et de la forêt décidue (voir Fig. 6). Aucune de ces cartes, cependant, n'a été établie—en ce qui concerne le secteur en question—à l'aide de travaux précis, comme ce fut le cas pour les régions plus à l'ouest et au sud.

Et justement, la comparaison avec les relevés effectués dans l'Indiana, le Maryland, le Michigan, l'Ohio nous font voir, dans les érablières, une composition floristique très différente de celle qui prévaut ici. Ces stations, cependant, retiennent en nombre suffisant les éléments considérés ici comme caractéristiques pour qu'on puisse croire à une simple vicariance méridionale d'une même association. Le Tableau I fait voir à la fois les similitudes et les dissemblances d'érablières du Québec, du Michigan (4), de l'Indiana (3), et du nord de l'Ontario (8). Dans les quatre régions, les observations portent sur un grand nombre de stations dans chacune desquelles se trouve l'érable à sucre. La région où chaque espèce atteint son maximum de fréquence nous a permis de les répartir en quatre catégories: (1) *éléments communs*, qui se trouvent à peu près dans les mêmes proportions dans toute l'aire; (2) *éléments exclusivement septentrionaux*, dont l'aire ne dépasse pas beaucoup la région laurentienne au sud, ou qui deviennent rares dans le Michigan et l'Indiana; (3) *éléments surtout septentrionaux*, dont la fréquence est beaucoup

TABLEAU I

Comparaison des éléments caractéristiques de l'érablière dans le Québec, dans l'Indiana (3), dans le Michigan (4), et dans le nord de l'Ontario (8)

Espèce	Pourcentages de présence					
	Québec	Indiana			Michigan	Batchawana
		1	2	3		
Éléments communs:						
Acer saccharophorum	100	100	100	100	100	+
Fagus grandifolia	70				100	
Tilia glabra	56				40	
Fraxinus americana	26				64	+
Botrychium virginianum	33	24	48	76		+
Arisaema atrorubens	23	90	100	100		
Asarum canadense	16	40	40	48		
Galium triflorum	22	52	68	72		+
Éléments surtout septentrionaux:						
Betula lutea	51					+
Sambucus pubens	32					+
Lonicera canadensis	9					+
Osmorrhiza Claytoni	22	4	4	4	20	
Smilacina racemosa	45	8	12	20	36	+
Sanguinaria canadensis	20	0	0	4		+
Uvularia grandiflora	27	4	4	4		
Éléments exclusivement septentrionaux:						
Abies balsamea	33					+
Acer pennsylvanicum	35					+
Cornus alternifolia	26					
Taxus canadensis	15					+
Viola eriocarpa	23					
Polygonatum pubescens	47					+
Trillium erectum	62					
Éléments surtout méridionaux:						
Quercus borealis	20				64	+
Celtis occidentalis	0.5	20	36	40		
Carpinus caroliniana	3	48	60	64	76	
Parthenocissus quinquefolia	4	100	100	100		
Ulmus fulva	6	76	76	92		
Geum canadense	1	72	84	92		
Viola papilionacea	2	80	84	96	20	
Éléments exclusivement méridionaux:						
Liriodendron tulipifera					64	
Asimina triloba		44	60	68	16	
Cercis canadensis		64	64	64		
Cornus florida		60	72	84	8	
Fraxinus lanceolata		96	100	100		
Nyssa sylvatica		60	96	80		
Benzoin aestivale		68	72	72	96	

plus grande dans le Québec et l'Ontario que dans l'Indiana et le Michigan; (4) *éléments surtout méridionaux*, qui atteignent ici leur limite nord mais sont plutôt rares; (5) *éléments exclusivement méridionaux*, qui ont leur limite nord bien au sud de notre aire. Il n'est guère possible de pousser plus loin

la comparaison pour l'instant. C'est d'ailleurs l'objet des présentes recherches que de fournir des documents descriptifs complets sur l'érablière de la région laurentienne et de dresser d'une façon précise le tableau de l'association. Il suffira donc de constater que l'aire sous observation présente un caractère convaincant d'homogénéité.

Définition et méthode

Les botanistes, les forestiers, les agronomes, les agriculteurs ont considéré jusqu'ici comme érablière—dans la région laurentienne—tout bois décidu où domine l'érable à sucre (*Acer saccharophorum* K. Koch[1]). Il n'y a généralement dans ces bois aucun conifère; mais on y trouve souvent le hêtre (*Fagus grandifolia*), le merisier (*Betula lutea*), la "plaine" (*Acer rubrum*), le tilleul (*Tilia glabra*), et quelques autres arbres. L'étage arbustif comprend le "bois barré" (*Acer pennsylvanicum*), le "bois d'orignal" (*Viburnum lantanoides*), et le noisetier (*Corylus cornuta*). Les plantes herbacées les plus remarquées sont sans doute les géophytes printanières qui fleurissent en grande abondance avant l'apparition des feuilles sur les arbres: trilles (*Trillium* spp.), claytonie (*Claytonia caroliniana*), ail-doux (*Erythronium americanum*), uvulaire (*Uvularia grandiflora*), etc. Sont également caractéristiques certaines composées (asters, prenanthes) qui fleurissent l'été, à un moment où la végétation herbacée devient moins abondante avec l'ombre épaisse du feuillage des arbres et la sécheresse relative des mois de juillet et d'août.

Les érablières occupent les sols bien drainés ordinairement assez profonds, à substratum sableux, franc ou même argileux. La couche superficielle est toujours fortement humifère et fraîche sans être humide. Le pH se tient ordinairement entre 6.2 et 7.5; il est donc neutre ou à peu près. Il est à remarquer qu'un écart de l'une ou de l'autre des conditions énumérées ci-dessus entraîne un changement floristique, de telle sorte qu'on n'a plus affaire à une érablière. La Fig. 1 donne un aperçu des principales formations arborescentes qu'on rencontre dans la région laurentienne, et dont la constitution est essentiellement conditionnée par la conjugaison du facteur sol et du facteur humidité ou drainage. On aura donc, selon le cas, une érablière, une sapinière (forêt canadienne), une cédraie, une pinède, une tourbière à épinette noire, une ormaie (formation alluviale, souvent inondée longuement au printemps, où dominent l'*Acer saccharinum*, l'*Ulmus americana*, le *Laportea canadensis*), une saulaie (où dominent le *Populus balsamifera*, *Salix* spp., *Desmodium canadense*).

Ce profil est basé sur les données d'observations générales mais très approximatives. Il serait important de la compléter par la détermination plus exacte de la réaction du sol qui est souvent un facteur déterminant. Ainsi, les cédraies sont de plusieurs sortes: marécageuses et peut-être acides ou sèches et reposant sur le calcaire.

[1] *Pour le nom Acer saccharophorum K. Koch employé de préférence à Acer saccharum Marshall, voir Rousseau, J., Contrib. Inst. Botan. Univ. Montréal, No 35, 1941.*

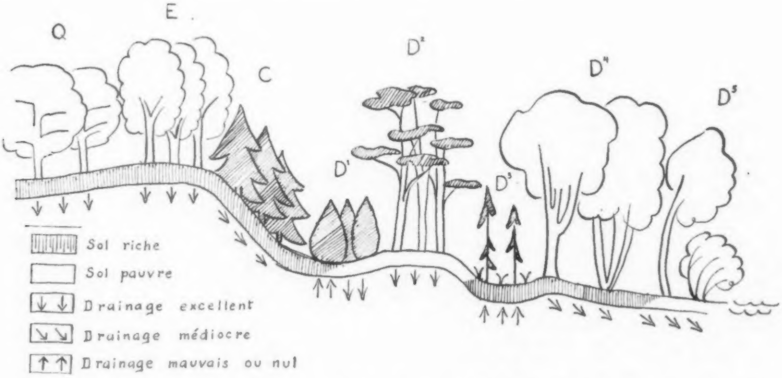

FIG. 1. *Q = chênaie (Quercus borealis); E = érablière (Acer saccharophorum, Fagus grandifolia); C = pessière (Picea glauca, Abies balsamea);* D^1 *= cédraie (Thuja occidentalis);* D^2 *= pinède (Pinus strobus, Viburnum acerifolium);* D^3 *= tourbière (Picea mariana, Kalmia angustifolia);* D^4 *= ormaie (Ulmus americana, Acer saccharinum);* D^5 *= saulaie (Populus balsamifera, Salix spp.).*

Il serait désirable de doubler ce schéma de celui des successions qui se partagent le même site à la faveur d'une destruction naturelle ou accidentelle; mais nous connaissons encore trop peu le dynamisme de ces associations pour nous aventurer plus loin pour l'instant.

Dans ces conditions écologiques bien définies, l'érablière est donc la formation végétale typique de la vallée moyenne du Saint-Laurent. On peut se la représenter comme couvrant toutes les collines des Cantons de l'Est, à l'exclusion des vallées à drainage lent, et du bord des cours d'eau. Elle s'étend dans toute la vallée du Richelieu et de l'Ottawa, sauf sur les alluvions sablonneuses et les amas de gravier qui forment de larges ceintures de pinèdes. Dans les cent premiers milles à l'intérieur de la chaîne des Laurentides, l'érablière est encore fréquente et forme avec la sapinière un damier irrégulier: elle occupe les sommets et les pentes bien drainés.

La valeur dynamique de l'érablière—même telle que définie très sommairement ci-dessus—semble bien être celle d'un climax. Dans l'aire qui nous occupe, il n'y a aucun doute quant à sa stabilité: elle se reproduit indéfiniment et elle est la seule association arborescente (toujours dans les conditions mentionnées plus haut) à le faire. Les botanistes qui ont herborisé dans cette région ont observé de nombreuses évidences de sa reconstruction spontanée.

Cent quatre-vingts relevés ont été faits dans la région laurentienne en 1940 et 1941. Ces relevés ont été faits en utilisant la méthode de Braun-Blanquet (1), et comportent des notes sur le sol, la hauteur des arbres et leur diamètre moyen, l'exposition et l'inclinaison du terrain, le pourcentage de couverture aux diverses strates de la végétation et une liste complète de toutes les espèces présentes avec un chiffre indiquant l'abondance et la sociabilité de chacune. Le quadrat était ordinairement de 200 mètres carrés

et circonscrivait une section homogène. Les bords des routes, les abords des cabanes à sucre, et des chemins de traverse ont été soigneusement évités.

La conception de l'association, ou de l'unité fondamentale de la phytosociologie, est l'objet d'un débat encore très vif parmi les écologistes. Plusieurs écoles se sont constituées, chacune proposant une méthode particulière et surtout reconnaissant comme valable un certain ordre de conclusions. Cela va du concept individuel de l'association de Gleason (6) jusqu'au système de hiérarchisation dynamique de Weaver et Clements (16) ou de Braun-Blanquet (1). Toutes les opinions sont sans doute permises et celle de chacun doit être respectée. Mais c'est aussi le devoir de tous les chercheurs d'améliorer les méthodes existantes ou tout au moins, de les appliquer en vue d'éliminer le plus possible les facteurs subjectifs.

C'est la raison pour laquelle cette étude de l'érablière laurentienne a été entreprise sur un matériel hétérogène. Dans tout travail scientifique les preuves les plus convaincantes sont assurément celles qui ressortent d'elles-mêmes des documents accumulés. De sorte qu'au lieu d'étudier seulement des érablières vierges, j'ai fait mes 180 relevés dans des bois où était présent l'érable à sucre. Beaucoup de ces bois se trouvaient dans des conditions plus ou moins normales: par exemple, l'humidité y était très prononcée, la pente très raide, la situation géographique nettement en dehors de l'aire principale, etc. De sorte qu'elles ne sauraient être considerées toutes comme typiques. D'autre part, un bon nombre avait subi les atteintes de la hache, de l'éclaircissage, du nettoyage, du feu, ou du pâturage. Ces dégradations—les premières naturelles, les secondes artificielles—ont été soigneusement notées dans chaque cas.

Les espèces ont été identifiées la plupart du temps sur le terrain par l'auteur et ses assistants. Cependant, quelque 900 récoltes ont été faites, surtout dans des groupes critiques. M. Jacques Rousseau a identifié les *Viola*, le R. F. Rolland-Germain les Graminées, et M. Marcel Raymond les *Carex*.

L'établissement d'un tableau d'association généralisé se fait essentiellement par la découverte des corrélations d'ordre écologique qui existent entre un certain nombre d'espèces que l'on nomme caractéristiques. Aussi l'identité de ces espèces est-elle l'objet principal des présentes recherches. Il a semblé plus sûr de travailler sur un matériel hétérogène, dans l'ignorance où nous sommes de la composition primitive du climax. Ainsi, il apparaîtra nettement si les espèces les plus fréquentes sont caractéristiques de l'état primitif et si d'autres le sont d'une forme prédominante de dégradation. Cela ressortira des corrélations écologiques auxquelles chaque espèce est soumise. Ainsi, aucun apriorisme n'a présidé aux investigations sur le terrain. La liste qui suit avec des annotations permettra, sans doute, aux espèces caractéristiques du climax en question de constituer un bloc à part dans l'ensemble des données recueillies et c'est ce bloc qui fournira la matière du tableau de l'association-type: *Aceretum saccharophori*. La connaissance des espèces et des conditions typiques permettront ensuite d'assortir les relevés selon leur "degré de

pureté" et de dresser un tableau où seront enfin exprimées les constantes et les corrélations écologiques et floristiques.

Caractérisation des espèces

Cinq considérations principales nous occupent au sujet de chacune des 346 espèces rencontrées dans les érablières au moins une fois: (1) la forme biologique à laquelle elles appartiennent; (2) leur pourcentage de présence dans l'ensemble des relevés; (3) leur degré de tolérance vis-à-vis de l'ombre; (4) leur mésophilie relative; (5) leur fidélité à l'association "érablière".

Formes biologiques

Ce sont celles que proposa d'abord Raunkiær (10) et qu'ont reprises la plupart des écologistes, dont Braun-Blanquet (1). Cette classification est basée sur la position des organes de régénération annuelle et elle ne peut qu'être très significative dans le cas d'une association soumise à un cycle annuel et à des variations saisonnières extrêmes. Comme il faut s'y attendre, les *thérophytes* (*Th*) sont presque absentes: un milieu fortement sciophile, riche en humus et très stable par ailleurs ne favorise guère les espèces annuelles qui n'y pénètrent que par accident et en très petit nombre. Les *géophytes* (*G*), à floraison rapide en pleine lumière et à organes de réserve souterrains très développés, trouvent là au contraire un milieu favorable et la majorité des géophytes laurentiennes ont pris refuge dans l'érablière. Les *hémicryptophytes* (*H*) sont largement caractéristiques des régions boréales humides; aussi celles de l'érablière doivent-elles leur prédilection pour cet habitat plutôt à leur mésophilie qu'à leur forme biologique. Quant aux *chaméphytes* (*Ch*), elles sont certainement plus nombreuses dans la forêt canadienne ou la toundra, et ne jouent pas ici un rôle appréciable. Les *phanérophytes* (*M* et *N*) sont sans doute une catégorie moins homogène que les précédentes et les espèces que nous rencontrons ici nous intéressent surtout au point de vue de la tolérance et de la distribution géographique générale.

Les formes biologiques des 346 espèces relevées ici se répartissent tel qu'indiqué au Tableau II. On peut constater que le spectre biologique se rapproche notablement de celui de l'Etat du Connecticut et ne correspond

TABLEAU II

SPECTRE BIOLOGIQUE DES 346 ESPÈCES RELEVÉES DANS L'ÉRABLIÈRE LAURENTIENNE COMPARÉ À CEUX D'AUTRES ASSOCIATIONS ET AU SPECTRE "NORMAL" (FLORE MONDIALE). CES DERNIERS, D'APRÈS BRAUN-BLANQUET (1)

	"Normal"	Suisse Centrale	Région Paris	Connecticut	Fagetum	Érablière
Phanérophytes	46	10	8	15	2	17
Chaméphytes	9	5	6.5	2	4	10
Hémicryptophytes	26	50	51.5	49	51.5	56
Géophytes	6	15	25	22	40.5	15
Thérophytes	13	20	9	12	2	2

guère à celui du *Fagetum* des Cévennes, le vicariant européen de l'érablière, pourtant. Ceci est dû à deux causes. La première est que le spectre biologique considéré seul n'a pas de signification précise. Braun-Blanquet (1, pp. 300, 301) fait remarquer que cet échantillonnage qualitatif donne une fausse image de la végétation d'un secteur ou d'une association, puisque le hêtre (*Fagus sylvatica*), qui conditionne l'existence même du *Fagetum* en question, ne compte que pour 2% dans le spectre, alors que le nombre des individus qui le représentent est très considérable. De même, dans la flore du Connecticut, une espèce très rare, ayant quelques dizaines de représentants, comptera autant que le chêne blanc, le tremble, l'hépatique, ou le pâturin répandus par millions sur tout le territoire.

Outre l'interprétation délicate du spectre biologique, il ne faut pas oublier la richesse relative de l'Amérique du Nord en arbres et arbustes (phanérophytes) par rapport à la pauvreté de la forêt européenne. Enfin, le spectre biologique des 346 espèces relevées ici se révélera sans doute assez différent du spectre de l'érablière typique une fois faite la sélection des relevés. Ainsi, la proportion des géophytes s'accroîtra certainement aux dépens des chaméphytes qui—comme on le verra plus loin (Tableaux III et IV)—ne sont guère des éléments importants dans l'écologie de l'érablière.

Présence

La liste des espèces rencontrées ayant été reportée sur un tableau, il devient possible d'établir pour chacune le pourcentage de présence par rapport aux 180 relevées. Cette liste, étant donné la méthode non-sélective suivie et décrite plus haut, rend compte d'une façon assez claire de la composition floristique moyenne des érablières laurentiennes dans leur état actuel.

Deux chiffres sont donnés pour chaque espèce: le pourcentage net de fréquence (sur 180 relevés) et la catégorie phytosociologique dans laquelle

FIG. 2

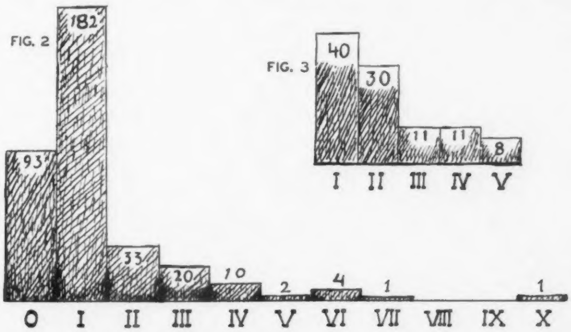

FIG. 2. *Diagramme de constance. Les chiffres au sommet des colonnes représentent (en ordonnées) le nombre d'espèces (sur 346) dans chaque classe phytosociologique. Celles-ci (en abscisses) ont les valeurs suivantes: I = présence dans 1 a 10% des 180 relevés: II dans 11 à 20%, etc.; 0 moins de 1% ou présence hors des quadrats.*

FIG. 3. *Diagramme de constance de l'Elynetum des Alpes, d'après Braun-Blanquet (1, p. 57).*

ce pourcentage les range. Ces catégories sont celles de Braun-Blanquet (1, p. 53) qui ont été subdivisées chacune en deux pour plus de précision. La catégorie 0 comprend les espèces présentes une fois seulement sur 180, donc ayant un pourcentage inférieur à 1%, ou encore les espèces trouvées seulement en dehors des quadrats mais sur leurs limites.

La Fig. 2 fait voir la répartition des espèces par classes ou le diagramme de constance. Une comparaison avec la Fig. 3, le diagramme de l'*Elynetum* des Alpes (1, p. 57), fait ressortir l'hétérogénéité de l'ensemble des relevés dans l'érablière laurentienne. Il est clair que les espèces appartenant à la catégorie 0 peuvent être éliminées complètement au point de vue écologique, leur rôle étant insignifiant. De même les espèces de la catégorie I ne sauraient être considérées—à quelques rares exceptions près—comme ayant une part quelconque à l'édification du climax. Ceci nous laissera donc vraisemblablement un diagramme assez semblable à celui de l'*Elynetum* (Fig. 3) dans sa forme générale. Il est à croire que les classes VIII et IX compteront quelques espèces quand le nombre total des relevés considérés ne sera plus de 180.

Sciophilie

La réaction des espèces à la lumière est un facteur très net d'élimination en ce qui concerne les caractéristiques de l'érablière. Il est évident qu'aucune héliophile ne saurait s'y introduire que par accident. Les géophytes qui fleurissent avant l'apparition des feuilles dans les arbres sont considérées comme sciophiles puisque la plus grande partie de leur cycle se poursuit dans l'ombre. Toutes les espèces, cependant, ne sont pas sciophiles pour la même raison. Les unes cherchent la facilité de la germination (*Acer saccharophorum*), les autres, l'humidité et la fraîcheur de l'air (*Dryopteris spinulosa*), ou bien la richesse du sol en humus (*Amphicarpaea bracteata*). D'autres enfin sont favorisées par la constance relative de la température—tant au cours de la période entière de végétation que du cycle quotidien—(*Athyrium angustum*), ou encore par la compétition réduite dans cet habitat plus exclusif (*Polygonatum pubescens*).

Il y a donc lieu de distinguer ici les plantes sciophiles (*S*), les plantes héliophiles (*L*), et les plantes indifférentes à la lumière (*I*) (voir Fig. 4). Il est bien entendu que ces distinctions ne sont pas toujours absolues et qu'une espèce sciophile peut quelquefois croître et se développer à la lumière ou dans l'ombre partielle. Aussi s'agit-il en ce moment de l'habitat *normal* de l'espèce, de celui où, généralement, dans l'aire en question, elle se trouve et *atteint son optimum de développement*. Je ne classifierai cependant ici, sous la désignation de sciophile (*S*), que les espèces qui se montrent pratiquement exclusives aux endroits ombragés. Ainsi, le *Cornus alternifolia* qui ne sort du bois que sur sa limite nord, là où l'ombre devient décidément trop froide, et l'*Aster acuminatus* qui se trouve dans les tourbières étroitement mêlé aux arbustes et compensant par l'humidité du sol et le durcissement de ses tissus l'excédent d'évaporation auquel il est soumis. Il conviendrait d'ailleurs de

vérifier dans tous les cas analogues si l'on n'a pas affaire à une forme ou tout au moins à une race écologique distincte.

Seront reconnues comme héliophiles (*L*) les espèces qui croissent habituellement en pleine lumière; c'est le cas de toutes les plantes de tourbière, de rochers, de prairies, et de pâturages. Elles sont ordinairement agressives et ont tendance à former des populations pures ou tout au moins très denses, lesquelles, étant donné leur intolérance, sont essentiellement transitoires. Cette catégorie comprend toutes les "mauvaises herbes", pour la plupart plantes introduites des pays méditerranéens. A l'héliophilie se joignent très souvent l'acidophilie et peu d'exigence quant à la richesse et même à la nature du sol. (Voir plus loin sous "mésophilie".) La catégorie des "indifférentes" (*I*) comprend des espèces qui se trouvent habituellement

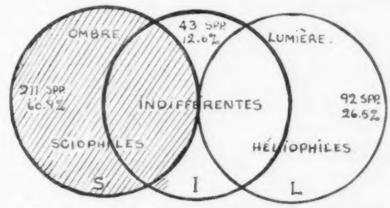

FIG. 4. *Réaction des espèces à la lumière.*

dans un habitat non franchement mésophytique, tel un bois clair de pin blanc (*Pinus strobus*) (voir Fig. 1 D^2), une formation alluviale ou riparienne (*Ulmus americana*, *Vitis vulpina*, *Anemone riparia*), des rochers abrités ou non (*Polypodium virginianum*). Il en est quelques-unes qui sont avant tout sensibles à un autre facteur et limité par lui, comme l'*Habenaria fimbriata* à l'humidité, l'*Eupatorium urticaefolium* à la richesse du sol, le *Pinus strobus* et le *Danthonia spicata* à son acidité. Toutes ces espèces s'accommodent fort bien de l'ombre, même si l'on ne peut pas dire qu'elles s'y trouvent nécessairement aussi bien que dans des habitats ouverts.

Sur 346 espèces, 211 sont sciophiles (soit $S = 60.9\%$), 43 sont indifférentes ($I = 12.6\%$), et 92 sont héliophiles ($L = 26.5\%$) (voir Fig. 4). Ce pourcentage élevé d'inadaptés (au moins 26.5%) est un coefficient d'hétérogénéité très démonstratif, et l'indice certain de la pénétration allogène.

Mésophilie

Il s'agit ici des limitations imposées par l'humidité. La Fig. 5 fait voir les catégories qu'on peut distinguer sous ce chapitre. Les classifications données par les auteurs (1, 5, 13, 16) quoique concordantes dans l'ensemble ne sont guère précises puisque les documents nous manquent à l'heure actuelle pour déterminer le minimum, l'optimum, et le maximum d'humidité spécifique. On a donné en attendant, à chaque espèce un status basé non pas sur ses virtualités, sa résistance, ou sa pression osmotique mais sur son habitat le plus commun. Ici, les deux extrêmes, plantes aquatiques et xérophiles proprement dites, ne nous intéressent pas.

A vrai dire, la mésophilie concerne à la fois le sol et l'air. L'érablière est un habitat mésophile parce que la richesse en matière organique de son sol en fait un excellent absorbant et lui confère un bon pouvoir de rétention de l'eau. D'autre part, la continuité de sa végétation depuis le sol jusqu'au faîte des arbres et la grande surface d'évaporation qu'on y trouve favorisent des espèces à tissus fragiles comme le *Dicentra cucullaria*, l'*Amphicarpaea bracteata*, et la plupart des fougères, qui ne résistent pas à l'évaporation rapide que cause un air sec, une grande chaleur, ou les rayons directs du soleil.

Les plantes de l'érablière sont donc mésophiles (*M*); elles trouvent leur optimum de développement dans un sol neutre aéré et frais sans être mouillé, dans une atmosphère relativement humide grâce à l'ombre et à de grandes surfaces d'évaporation continue. Ces plantes sont plus ou moins intolérantes d'un excès d'humidité ou de sécheresse.

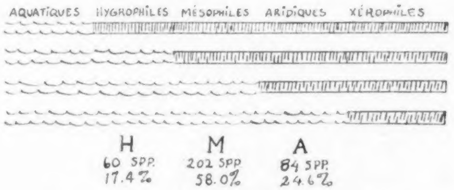

FIG. 5. *Réaction des espèces à l'humidité.*

Cependant, à cause de conditions locales du microclimat, certaines hygrophiles (*H*) sont assez fréquentes dans l'érablière: *Dirca palustris*, *Laportea canadensis*, *Arisaema atrorubens*, *Onoclea sensibilis*, *Impatiens biflora*. A ces espèces il faut un sol saturé d'eau, au moins pendant une partie importante de leur cycle. Elles sont assez sensibles à ce facteur pour disparaître tout-à-fait, si l'humidité du sol décroît par drainage ou si un assèchement superficiel résulte de la suppression partielle de l'étage arborescent.

L'autre extrême est représenté par les espèces aridiques (*A*), dont le nombre est très considérable puisque ce sont par excellence des plantes qui envahissent une érablière dégradée. Outre qu'elles sont peu exigeantes en eau (sans être de véritables xérophiles, comme les *Sedum*, les *Elymus*, le *Mertensia maritima*, et à plus forte raison les *Opuntia*, les *Cereus*, les *Stapelia*), elles se trouvent bien d'un éclairage augmenté et d'une fertilité même très réduite qui élimine la compétition. La plupart sont acidophiles. Ce sont, en partie, des espèces étrangères, appartenant au climat méditerranéen. Aussi, dès les premiers stades de reconstruction naturelle de l'érablière ne peuvent-elles tenir tête à la concurrence des espèces indigènes. Elles sont essentiellement intolérantes, et déplacées sitôt que l'évolution du sol hausse le pH et augmente le pourcentage de matière organique.

Certes, ce facteur d'humidité est étroitement corrélatif à la température et à la latitude: telle hygrophile dans la région de Montréal (*Kalmia angusti-*

folia) devient mésophile sur la côte nord du Golfe Saint-Laurent; telle mésophile en Abitibi et jusque dans nos régions (*Trillium cernuum*, *Cornus canadensis*) se trouve dans des endroits plus humides aux Etats-Unis. La même équivalence existe avec l'altitude, comme dans le cas de l'*Acer spicatum*, et du *Luzula saltuensis* présents ici au niveau de la mer et relégués aux sommets dans la Caroline.

La proportion des trois catégories en présence est comme suit: mésophiles, 202 (M = 58.0%), hygrophiles, 60 (H = 17.4%), et aridiques, 84 (A = 24.6%) (voir Fig. 5). Comme dans le cas précédent, le caractère propre au milieu (mésophilie) domine, mais le pourcentage relativement élevé d'aridiques est le coefficient de dégradation.

Fidélité

Il est difficile de donner ici une classification aussi nette que pour les deux facteurs précédents. Il s'agit, en effet, de déterminer à quelle association chaque espèce appartient en propre. Or, les auteurs nous renseignent le plus souvent sur le seul habitat, et les études compréhensives de phytosociologie manquent encore. Britton et Brown (2), Robinson et Fernald (12), et Marie-Victorin (9) nous donnent cependant de très précieux points de repère. Dans certains cas, cependant, la distribution géographique générale d'une espèce peut être trompeuse. Pour ne citer que l'exemple de l'érable à sucre, son aire dépasse de beaucoup celle de l'érablière, tout comme l'aire du *Cornus canadensis* dépasse de beaucoup celle du *Piceetum*. Mes observations personnelles sur le terrain—et surtout au cours des deux dernières années, avec un objet précis en vue—m'auront surtout servi à établir la présente classification écologique (sciophilie et mésophilie) et phytosociologique (fidélité).

On entend par fidélité (1, pp. 58-59) la constance avec laquelle une espèce se trouve dans un habitat ou une association à l'exclusion des autres habitats ou associations dans un secteur géographique donné. A ce point de vue, nous distinguons:

(*E*) les espèces exclusives à l'érablière (voir Fig. 1E);

(*C*) les espèces communes à l'érablière et à la forêt canadienne ou caractéristiques de celle-ci (voir Fig. 1C);

(*Q*) les espèces communes à l'érablière et aux associations méridionales arborescentes et mésophiles (*Quercetum*, *Hicorietum*, etc.) ou caractéristiques de celles-ci (voir Fig. 1Q);

(*D*) les espèces propres ou caractéristiques d'autres habitats dans les limites géographiques de l'érablière laurentienne; rivages (voir Fig. 1D^4 et D^5), tourbières (Fig. 1D^3), marécages, prairies, bois clairs ou mixtes (de transition), pinèdes (Fig. 1D^2), cédraies (Fig. 1D^1);

(*U*) les espèces ubiquistes, souvent adventices, agressives, et abondantes dans les lieux vagues, les fossés, les terrains pauvres, et sans préférences écologiques marquées.

Les espèces exclusives à l'érablière ne se rencontrent guère dans d'autres habitats et n'y trouvent pas, de toutes façons, leur optimum de développement et d'expansion. Il faut les croire extrêmement sensibles à l'équilibre *température-variation-saisonnière-humidité-ombre* défini plus haut et spécialisées au point de survivre difficilement dans un autre milieu. Certes, sur les limites de leur aire, il peut leur arriver d'en sortir mais ce ne seront là que de faibles extensions où d'autres conjonctions de facteurs (altitude et humidité pour l'érable à sucre vers le sud; humidité du sol pour certaines fougères; chaleur du soleil pour le *Cornus alternifolia* au nord) compensent la dégradation de l'équilibre optimum de l'érablière dans son aire principale.

Parmi les espèces communes à l'érablière et à la forêt canadienne viennent en premier lieu celles qui sont caractéristiques de la sère septentrionale, comme les épinettes, les quatre-temps (*Cornus canadensis*), la surette des bois (*Oxalis montana*), et qui ne se rencontrent que par accident dans les bois décidus. D'autres cependant sont à la fois si fréquentes et si abondantes, comme le maianthème (*Maianthemum canadense*), le *Dryopteris spinulosa*, qu'on peut les croire également adaptées aux deux climax. Cette distinction n'est toutefois pas très facile à faire pour l'instant, en l'absence de données quantitatives aussi précises pour la forêt canadienne que celles que je présente ici pour l'érablière. En attendant, il paraît légitime de considérer les espèces rangées dans la présente catégorie comme trouvant leur optimum dans la forêt canadienne. Pour certaines, d'ailleurs, l'érablière n'est guère que le meilleur refuge offert à des espèces sur leur limite sud.

Les mêmes considérations et relations se vérifient en ce qui concerne respectivement l'érablière et les forêts décidues méridionales que dominent les chênes (*Quercus* spp.) ou les noyers tendres (*Carya* spp.). Peu d'espèces, d'ailleurs, par leur degré de présence élevé paraissent pouvoir être considérées comme réellement communes aux deux climax: peut-être le bois-de-fer (*Ostrya virginiana*) et la sanicule trifoliée (*Sanicula trifolia*). La plupart des autres font figure d'excentriques, c'est-à-dire d'espèces sur la limite nord de leur aire, comme l'érable noir (*Acer nigrum*), le bouleau merisier (*Betula lenta*), les *Dryopteris Goldiana*, et *Carex normalis*.

Les plantes ordinairement limitées à d'autres habitats portent déjà la mention d'héliophiles (*Populus tremuloides, Desmodium canadense*) ou d'hygrophiles (*Geum rivale, Impatiens biflora, Onoclea sensibilis*). Plusieurs font partie de la sère de l'érablière, étant liées à un stade de dégradation (*Betula papyrifera, Carex scoparia*) ou de construction (*Pinus strobus, Danthonia spicata*). La présence dans l'érablière de l'une quelconque de ces espèces, surtout si elle est abondante, est un signe certain d'immaturité ou de dégradation naturelle ou artificielle.

Le groupe des ubiquistes, pour la plupart rudérales, "mauvaises herbes" introduites d'autres régions, surtout européennes, se compose d'espèces excessivement agressives et le plus souvent grégaires. Leur dissémination par reproduction ou par bourgeonnement est très rapide et elles sont par excellence aptes à combler en un temps record tout vide écologique. C'est pourquoi

leur présence locale dans une érablière n'est pas nécessairement très significative, puisqu'elles profitent d'une brèche étroite pour s'introduire, sans jouer un rôle écologique appréciable. Par contre, si elles sont nombreuses et d'une distribution homogène dans une parcelle, il n'y a pas de signe plus certain de dégradation artificielle. Elles marchent comme une armée sur les traces du feu; elles suivent aussi patiemment la hache, la dent des animaux domestiques, la charrue, et les roues des voitures. Mais elles ne peuvent guère entamer l'équilibre naturel et virginal de l'érablière même si le vent, les hommes, ou les animaux y portent leurs semences.

Sur 346 espèces, 76 sont exclusivement de l'érablière (E = 21.7%), 70 sont communes avec la forêt canadienne (C = 20.2%), 36 sont communes avec les forêt mésophiles méridionales (Q = 10.4%), 131 appartiennent à d'autres habitats (D = 37.9%), et 33 sont des mauvaises herbes (U = 9.8%). Les espèces dont la valeur est constructive sont donc ($E + C + Q$) 52.3% du *total* et les éléments négatifs constituent 47.7%. Ceci ne nous donne encore aucun indice de la dégradation moyenne des érablières de la région laurentienne, ni du pourcentage des érablières dégradées. Seule la distribution de ces éléments dans les 180 érablières étudiées nous renseignera là-dessus.

Liste annotée des espèces

Les 346 espèces sont présentées dans les Tableaux III à IX selon un ordre qui suit leur valeur comme indice. Il a paru pratique d'assigner aux catégories des valeurs équivalentes à celles dont on se sert pour marquer d'une façon quantitative l'abondance, la sociabilité, la fidélité (1).

Chaque nom d'espèce est précédé d'un symbole se rapportant à une forme biologique (voir p. 72): *M:* macrophanérophyte (arbre), *N:* nanophanérophyte (arbuste), *Ch:* chaméphyte, *H:* hémicryptophyte, *G:* géophyte, *Th:* thérophyte (annuelle).

Le nom de l'espèce est suivi d'une formule de trois lettres. La première se rapporte au comportement de l'espèce vis-à-vis de la lumière et présente trois alternatives (voir p. 74 et Fig. 4): *S:* sciophile, *I:* indifférente, *L:* héliophile.

La seconde a trait à la réaction de l'espèce à l'humidité et comporte également trois alternatives (voir p. 76 et Fig. 5): *H:* hygrophile, *M:* mésophile, *A:* aridique.

La troisième détermine la fidélité par rapport à l'érablière et comporte cinq alternatives (voir p. 77 et Fig. 1): *E:* exclusive à l'érablière, *C:* commune à la forêt canadienne et à l'érablière, *Q:* commune à la forêt méridionale et à l'érablière, *D:* propre à un tout autre habitat, *U:* ubiquiste.

Cette formule est suivie de deux chiffres dont le premier (arabe) exprime le pourcentage de présence et le second (romain) la classe phytosociologique à laquelle il appartient (voir p. 73 et Fig. 2).

Pour les raisons exposées plus haut, il est clair que dans chaque série de caractères, il y a une alternative qui présente un facteur favorable à l'associ-

TABLEAU III

INDICE 5

ESPÈCES SCIOPHILES (*S*), MÉSOPHILES (*M*), ET FIDÈLES À L'ÉRABLIÈRE (*E*).
(VOIR FIG. 1, 4, 5, ET TEXTE)

Forme biologique	Espèce	Formule écologique	Pourcentage de présence	Classe phyto-sociologique
M	*Acer saccharophorum*	*SME*	100	X
M	*Fagus grandifolia*	*SME*	70	VII
M	*Tilia glabra*	*SME*	56	VI
M	*Betula lutea*	*SME*	51	VI
M	*Fraxinus americana*	*SME*	26	III
M	*Tsuga canadensis*	*SME*	22	III
N	*Acer pennsylvanicum*	*SME*	35	IV
N	*Corylus cornuta*	*SME*	33	IV
N	*Sambucus pubens*	*SME*	32	IV
N	*Viburnum lantanoides*	*SME*	28	III
N	*Cornus alternifolia*	*SME*	26	III
N	*Lonicera canadensis*	*SME*	9	I
N	*Rubus odoratus*	*SME*	8	I
Ch	*Ribes Cynosbati*	*SME*	1	I
H	*Viola eriocarpa*	*SME*	23	III
H	*Viola canadensis*	*SME*	22	III
H	*Osmorrhiza Claytoni*	*SME*	22	III
H	*Hepatica acutiloba*	*SME*	20	II
H	*Asarum canadense*	*SME*	16	II
H	*Carex pedunculata*	*SME*	14	II
H	*Mitella diphylla*	*SME*	12	II
H	*Aralia racemosa*	*SME*	12	II
H	*Thalictrum dioicum*	*SME*	12	II
H	*Carex arctata*	*SME*	12	II
H	*Hydrophyllum virginianum*	*SME*	11	II
H	*Solidago latifolia*	*SME*	11	II
H	*Dilepyrum erectum*	*SME*	11	II
H	*Carex plantaginea*	*SME*	10	I
H	*Solidago caesia*	*SME*	9	I
H	*Actaea* sp.	*SME*	9	I
H	*Actaea pachypoda*	*SME*	8	I
H	*Carex Deweyana*	*SME*	8	I
H	*Amphicarpaea bracteata*	*SME*	7	I
H	*Desmodium grandiflorum*	*SME*	7	I
H	*Viola pubescens*	*SME*	5	I
H	*Carex radiata*	*SME*	4	I
H	*Carex albursina*	*SME*	4	I
H	*Sanicula* sp.	*SME*	4	I
H	*Sanicula trifoliata*	*SME*	3	I
H	*Actaea rubra*	*SME*	3	I
H	*Actaea alba*	*SME*	3	I
H	*Carex gracillima*	*SME*	3	I
H	*Carex leptonervia*	*SME*	2	I
H	*Carex novae-angliae*	*SME*	2	I
H	*Viola papilionacea*	*SME*	2	I
H	*Carex blanda*	*SME*	2	I
H	*Cypripedium Calceolus*	*SME*	1	I
H	*Carex anceps*	*SME*	1	I
H	*Osmorrhiza longistylis*	*SME*	0.5	0
H	*Epifagus virginiana*	*SME*	0.5	0
H	*Carex rosea*	*SME*	0.5	0
H	*Carex convoluta*	*SME*	0.5	0
H	*Carex bromoides*	*SME*	0.5	0

TABLEAU III—*fin*

INDICE 5

ESPÈCES SCIOPHILES (*S*), MÉSOPHILES (*M*), ET FIDÈLES À L'ÉRABLIÈRE (*E*). (VOIR FIG. 1, 4, 5, ET TEXTE)—*fin*

Forme biologique	Espèce	Formule écologique	Pourcentage de présence	Classe phyto-sociologique
H	*Orchis spectabilis*	*SME*	0	0
G	*Trillium erectum*	*SME*	62	VII
G	*Polygonatum pubescens*	*SME*	47	V
G	*Smilacina racemosa*	*SME*	45	V
G	*Erythronium americanum*	*SME*	35	IV
G	*Botrychium virginianum*	*SME*	33	IV
G	*Uvularia grandiflora*	*SME*	27	III
G	*Trillium grandiflorum*	*SME*	27	III
G	*Caulophyllum thalictroides*	*SME*	26	III
G	*Sanguinaria canadensis*	*SME*	20	II
G	*Dryopteris noveboracensis*	*SME*	16	II
G	*Adiantum pedatum*	*SME*	14	II
G	*Allium tricoccum*	*SME*	14	II
G	*Claytonia caroliniana*	*SME*	14	II
G	*Polystichum acrostichoides*	*SME*	11	II
G	*Dentaria diphylla*	*SME*	9	I
G	*Dicentra Cucullaria*	*SME*	9	I
G	*Dicentra canadensis*	*SME*	5	I
G	*Dryopteris Goldiana*	*SME*	3	I

ation "érablière". Ce sont la sciophilie (*S*), la mésophilie (*M*), et la fidélité sociologique (*E*). Les autres alternatives caractérisent pour chaque espèce un écart plus ou moins grave de cette formule *SME* et par conséquent une aptitude moindre à jouer un rôle dans cette association.

Il y avait 45 combinaisons théoriquement possibles de ces trois séries de caractères, dont 15 seulement se sont réalisées dans la pratique. Nous avons donc, aux deux pôles, pour ainsi dire, les formules *SME* et *LAU*. On peut reconnaître ainsi trois ordres de caractères: (1) *S*, *M*, *E*, facteurs *primaires* ou de *construction* de l'érablière; (2) *I*, *H*, *C*, *Q*, facteurs *secondaires* ou de *dégradation naturelle* ou de *variation écologique;* (3) *L*, *A*, *D*, *U*, facteurs *tertiaires* ou de *dégradation artificielle.* La valeur de chaque formule pourra donc être tablée d'après cette norme et comme il apparaît aux Tableaux III à IX.

Indice 5

Le Tableau III est celui des 72 espèces tolérantes et mésophiles dont la distribution est restreinte à l'érablière et parmi lesquelles seront choisies les caractéristiques qui serviront de base à la définition de l'*Aceretum saccharophori.* C'est ici qu'apparaissent le plus nettement les distinctions entre les données de l'écologie et de la phytosociologie. Des espèces comme l'*Epifagus virginiana* et le *Dicentra canadensis* ne se rencontrent strictement jamais en dehors de l'érablière, mais elles ne se sont trouvées respectivement que dans moins de un pour cent et cinq pour cent des relevés. Il faut donc croire

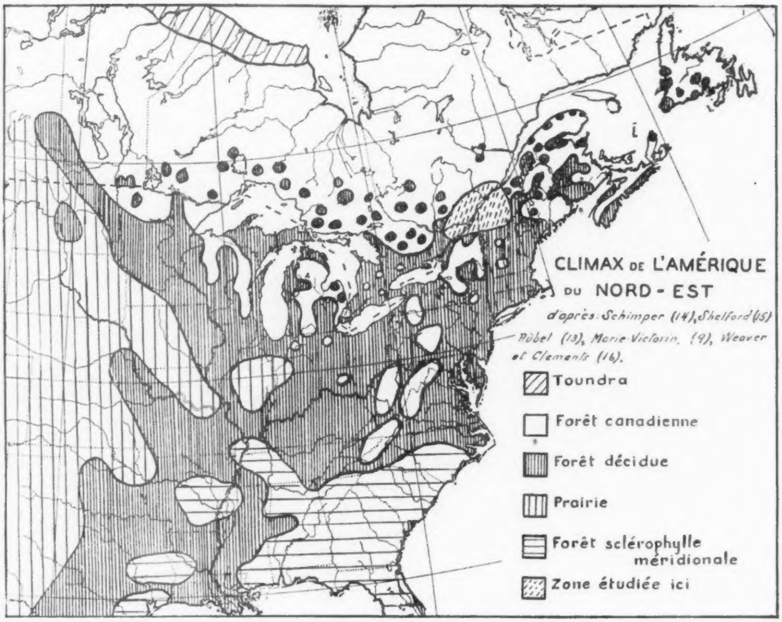

FIG. 6.

que, malgré leur excellente adaptation au milieu en question, ces espèces n'ont pas *réussi*, puisqu'elles manquent si souvent à l'habitat qui leur est favorable. Il faut les croire aussi moins bonnes caractéristiques que d'autres espèces, moins spécialisées, plus plastiques, moins exclusives mais plus souvent présentes (comme, par exemple, le *Dryopteris spinulosa*: voir Tableau IV). Il faut se rappeler que les pourcentages indiqués ici varieront nécessairement sur le tableau définitif de l'association, puisqu'alors un nombre plus restreint de relevés homogènes sera considéré.

Indice 4

Le Tableau IV réunit trois formules contenant chacune deux facteurs primaires et un facteur secondaire. L'on voit ici les deux grandes influences phytosociologiques opposées qui s'attaquent à l'érablière: les forêts septentrionale et méridionale. Il est tout-à-fait évident que l'influence de la forêt canadienne est la plus prononcée; nous en avons ici la preuve statistique: 68 espèces y pénètrent contre 36 de la forêt méridionale. D'ailleurs la Fig. 6 fait bien voir combien plus près de la sphère d'influence de la forêt canadienne se trouve l'érablière laurentienne que de celle de la forêt méridionale.

Assurément, les espèces représentées ici avec la formule *SMC* sont l'indice de conditions locales plus froides, souvent parce que plus humides, moins bien drainées. Pour beaucoup d'espèces les chiffres présentés ici sont une preuve intéressante de plasticité. Ainsi le *Linnaea borealis* et le *Gaultheria*

TABLEAU IV

Indice 4

Espèces de la forêt canadienne (*SMC*), de la forêt décidue méridionale (*SMQ*), ou des érablières humides (*SHE*)

Forme biologique	Espèce	Formule écologique	Pourcentage de présence	Classe phyto-sociologique
M	*Abies balsamea*	*SMC*	33	IV
M	*Picea glauca*	*SMC*	7	I
M	*Picea mariana*	*SMC*	4	I
M	*Sorbus americana*	*SMC*	4	I
M	*Picea rubens*	*SMC*	2	I
N	*Acer spicatum*	*SMC*	22	III
N	†*Cornus Amomum*	*SMC*	0.5	0
Ch	*Taxus canadensis*	*SMC*	15	II
Ch	*Lycopodium lucidulum*	*SMC*	15	II
Ch	*Mitchella repens*	*SMC*	12	II
Ch	*Lycopodium obscurum*	*SMC*	9	I
Ch	*Pyrola elliptica*	*SMC*	5	I
Ch	*Ribes americanum*	*SMC*	4	I
Ch	*Pyrola secunda*	*SMC*	3	I
Ch	*Ribes triste*	*SMC*	2	I
Ch	†*Pyrola asarifolia*	*SMC*	1	I
Ch	*Ribes glandulosum*	*SMC*	1	I
Ch	*Cornus canadensis*	*SMC*	1	I
Ch	*Lycopodium complanatum*	*SMC*	1	I
Ch	*Lycopodium flabelliforme*	*SMC*	1	I
Ch	*Lycopodium clavatum*	*SMC*	1	I
Ch	*Lycopodium annotinum*	*SMC*	1	I
Ch	*Ribes lacustre*	*SMC*	0.5	0
Ch	*Gaultheria procumbens*	*SMC*	0.5	0
Ch	*Chimaphila umbellata*	*SMC*	0	0
Ch	*Linnaea borealis*	*SMC*	0	0
Ch	*Chiogenes hispidula*	*SMC*	0	0
H	*Tiarella cordifolia*	*SMC*	34	IV
H	*Galium triflorum*	*SMC*	22	III
H	*Trientalis borealis*	*SMC*	22	III
H	*Prenanthes* sp.	*SMC*	22	III
H	*Rubus pubescens*	*SMC*	17	II
H	*Clintonia borealis*	*SMC*	16	II
H	*Aster acuminatus*	*SMC*	16	II
H	*Prenanthes trifoliata*	*SMC*	11	II
H	*Viola incognita*	*SMC*	8	I
H	*Viola septentrionalis*	*SMC*	7	I
H	*Prenanthes altissima*	*SMC*	4	I
H	*Coptis groenlandica*	*SMC*	3	I
H	*Oxalis montana*	*SMC*	2	I
H	*Athyrium thelypteroides*	*SMC*	2	I
H	*Athyrium pycnocarpon*	*SMC*	2	I
H	*Equisetum scirpoides*	*SMC*	2	I
H	†*Mitella nuda*	*SMC*	2	I
H	*Viola nephrophylla*	*SMC*	1	I
H	*Dalibarda repens*	*SMC*	1	I
H	*Cypripedium acaule*	*SMC*	1	I
H	*Viola Selkirkii*	*SMC*	0.5	0
H	*Carex stellulata*	*SMC*	0.5	0
H	*Luzula saltuensis*	*SMC*	0.5	0
H	*Monotropa uniflora*	*SMC*	0.5	0
H	*Solidago macrophylla*	*SMC*	0.5	0

† *Signifie en dehors de l'aire indiquée par les lignes brisées dans la Fig. 6.*

TABLEAU IV—*fin*

INDICE 4

ESPÈCES DE LA FORÊT CANADIENNE (*SMC*), DE LA FORÊT DÉCIDUE MÉRIDIONALE (*SMQ*), OU DES ÉRABLIÈRES HUMIDES (*SHE*)—*fin*

Forme biologique	Espèce	Formule écologique	Pourcentage de présence	Classe phyto-sociologique
G	*Dryopteris spinulosa*	*SMC*	53	VI
G	*Aralia nudicaulis*	*SMC*	36	IV
G	*Maianthemum canadense*	*SMC*	34	IV
G	*Streptopus roseus*	*SMC*	34	IV
G	*Athyrium angustum*	*SMC*	30	III
G	*Medeola virginiana*	*SMC*	16	II
G	*Dryopteris marginalis*	*SMC*	15	II
G	*Dryopteris Linnaeana*	*SMC*	13	II
G	*Trillium undulatum*	*SMC*	13	II
G	*Dryopteris Phegopteris*	*SMC*	5	I
G	*Trillium cernuum*	*SMC*	1	I
G	*Polystichum Braunii*	*SMC*	0.5	0
G	†*Dryopteris Filix-mas*	*SMC*	0.5	0
G	†*Streptopus oreopolus*	*SMC*	0.5	0
G	*Corallorhiza maculata*	*SMC*	0.5	0
Th	*Halenia deflexa*	*SMC*	0.5	0
M	*Ostrya virginiana*	*SMQ*	28	III
M	*Carya ovata*	*SMQ*	13	II
M	*Prunus serotina*	*SMQ*	6	I
M	[n]*Betula lenta*	*SMQ*	5	I
M	[n]*Juglans cinerea*	*SMQ*	5	I
M	[n]*Acer nigrum*	*SMQ*	4	I
M	*Carya cordiformis*	*SMQ*	4	I
M	[n]*Carpinus caroliniana*	*SMQ*	3	I
M	[n]*Quercus alba*	*SMQ*	3	I
M	[n]*Quercus macrocarpa*	*SMQ*	1	I
M	[n]*Tilia neglecta*	*SMQ*	1	I
M	[n]*Quercus bicolor*	*SMQ*	1	I
M	[n]*Celtis occidentalis*	*SMQ*	0.5	0
M	†*Quercus ilicifolia*	*SMQ*	0.5	0
N	*Celastrus scandens*	*SMQ*	3	I
N	[n]*Hamamelis virginiana*	*SMQ*	2	I
H	[n]*Parthenocissus quinquefolia*	*SMQ*	4	I
H	*Poa alsodes*	*SMQ*	4	I
H	*Sanicula gregaria*	*SMQ*	2	I
H	*Galium lanceolatum*	*SMQ*	2	I
H	[n]*Smilax herbacea*	*SMQ*	2	I
H	*Phryma leptostachya*	*SMQ*	2	I
H	[n]*Hepatica americana*	*SMQ*	1	I
H	[n]*Parthenocissus vitacea*	*SMQ*	2	I
H	*Carex normalis*	*SMQ*	2	I
H	*Geum canadense*	*SMQ*	1	I
H	[n]*Viola rotundifolia*	*SMQ*	1	I
H	[n]*Viola rostrata*	*SMQ*	1	I
H	*Cryptotaenia canadensis*	*SMQ*	0.5	0
H	[n]*Polygonum virginianum*	*SMQ*	0	0
H	[n]*Triosteum aurantiacum*	*SMQ*	0.5	0
N	*Dirca palustris*	*SHE*	10	I
H	*Circaea latifolia*	*SHE*	9	I
G	*Arisaema atrorubens*	*SHE*	23	III
G	*Habenaria bracteata*	*SHE*	0	0

† *Signifie en dehors de l'aire indiquée par les lignes brisées dans la Fig. 6.*

[n] *Espèces sur leur limite nord.*

procumbens atteignent sensiblement la même latitude sud que le *Maianthemum canadense*, l'*Abies balsamea*, ou le *Taxus canadensis*, mais sont loin de pénétrer aussi souvent dans la forêt décidue. D'autres espèces sont ici dans une sorte d'habitat moyen, comme l'*Acer spicatum* et le *Luzula saltuensis*, hôtes habituels des latitudes boréales et réfugiés en altitude dans les montagnes caroliniennes.

Les espèces qui ont les formules *SMQ*, sauf l'*Ostrya virginiana*, le *Carya ovata*, l'*Uvularia sessilifolia* sont plutôt accidentelles dans l'aire laurentienne de l'érablière. Elles touchent ici à leur limite septentrionale de distribution: un grand nombre atteignent même cette limite quelque part à l'intérieur même de la région étudiée: *Celtis occidentalis*, *Acer nigrum*, *Hamamelis virginiana*, *Smilax herbacea*, *Polygonum virginianum*, *Claytonia virginica* ne dépassent pas de beaucoup l'archipel d'Hochelaga.

Une troisième formule *SHE* ne réunit que quatre espèces. Celles-ci se distinguent de celles du Tableau III en étant sur les limites extrêmes de la mésophilie. Leur exigence en humidité dépasse nettement les conditions ordinaires de l'érablière.

Indice 3

La liste du Tableau V—deux caractères primaires et un tertiaire—est très courte. En effet, les plantes franchement sciophiles et mésophiles qui n'appartiennent écologiquement ni à l'érablière, ni à la forêt canadienne, ni à la forêt décidue méridionale sont plutôt rares. Les espèces des bois secondaires de bouleau ou de tremble ne sont guère sciophiles, encore moins mésophiles. La même chose est vraie des espèces de la pinède et de la cédraie. Les trois

TABLEAU V

INDICE 3

ESPÈCES SCIOPHILES (*S*) ET MÉSOPHILES (*M*) MAIS D'UN AUTRE HABITAT (*D*) QUE L'ÉRABLIÈRE

Forme biologique	Espèce	Formule écologique	Pourcentage de présence	Classe phyto-sociologique
M	*Acer rubrum*	*SMD*	35	IV
M	*Ulmus americana*	*SMD*	28	III
M	*Quercus borealis*	*SMD*	20	II
N	*Zanthoxylum americanum*	*SMD*	2	I
Ch	*Rubus canadensis*	*SMD*	0	0
H	*Viola renifolia*	*SMD*	6	I
H	*Aster macrophyllus*	*SMD*	5	I
H	*Oryzopsis asperifolia*	*SMD*	1	I
H	*Verbena urticaefolia*	*SMD*	1	I
H	*Viola sororia*	*SMD*	0.5	0
H	*Viola conspersa*	*SMD*	0.5	0
G	**Epipactis latifolia*	*SMD*	3	I

* *Espèce naturalisée.*

arbres qui y figurent se rencontrent très fréquemment dans l'érablière. Je les crois, cependant, caractéristiques d'un tout autre groupement. La chênaie est représentée dans la région étudiée ici par des ilôts (Fig. 1Q) dont quelques-uns sont assez importants, notamment sur les Montérégiennes et

TABLEAU VI

INDICE 2

ESPÈCES DE PEU DE VALEUR CONSTRUCTIVE POUR L'ÉRABLIÈRE. (*SHC*): SCIOPHILES, HYDROPHILES DE LA FORÊT CANADIENNE; (*SHD*): SCIOPHILES, HYDROPHILES D'HABITATS DIVERS; (*IMD*): INDIFFÉRENTES À LA LUMIÈRE, MÉSOPHILES D'HABITATS DIVERS; (*LMD*): HÉLIOPHILES MÉSOPHYTIQUES D'HABITATS DIVERS

Forme biologique	Espèce	Formule écologique	Pourcentage de présence	Classe phyto-sociologique
H	*Circaea alpina*	*SHC*	6	I
G	*Osmunda cinnamomea*	*SHC*	7	I
M	ⁿ*Acer saccharinum*	*SHD*	2	I
H	*Laportea canadensis*	*SHD*	12	II
H	*Panax trifolium*	*SHD*	5	I
H	*Impatiens biflora*	*SHD*	4	I
H	*Ranunculus abortivus*	*SHD*	4	I
H	*Cystopteris bulbifera*	*SHD*	4	I
H	*Cystopteris fragilis*	*SHD*	1	I
H	*Viola cucullata*	*SHD*	1	I
H	*Impatiens* sp.	*SHD*	1	I
H	*Hydrocotyle americana*	*SHD*	0.5	0
H	*Carex scabrata*	*SHD*	0.5	0
H	**Hypericum punctatum*	*SHD*	0.5	0
G	*Osmunda Claytoniana*	*SHD*	7	I
G	*Onoclea sensibilis*	*SHD*	7	I
G	*Pteretis nodulosa*	*SHD*	3	I
G	ⁿ*Symplocarpus foetidus*	*SHD*	0.5	0
G	*Habenaria fimbriata*	*SHD*	0.5	0
M	ⁿ*Ulmus fulva*	*IMD*	6	I
M	ⁿ*Ulmus racemosa*	*IMD*	0.5	0
H	*Carex flexuosa*	*IMD*	3	I
H	*Carex tribuloides*	*IMD*	3	I
H	ⁿ*Vitis vulpina*	*IMD*	2	I
H	*Veratrum viride*	*IMD*	2	I
H	*Poa nemoralis*	*IMD*	2	I
H	*Eupatorium urticaefolium*	*IMD*	1	I
H	*Poa palustris*	*IMD*	1	I
H	ⁿ*Menispermum canadense*	*IMD*	0.5	0
H	*Saxifraga virginiensis*	*IMD*	0.5	0
N	*Cornus stolonifera*	*LMD*	1	I
Ch	*Rubus occidentalis*	*LMD*	8	I
H	*Anemone cylindrica*	*LMD*	0.5	0

* *Naturalisée.*

ⁿ *Espèce sur sa limite nord.*

dans la vallée inférieure de l'Outaouais. D'autre part, l'orme d'Amérique et la "plaine" sont sans doute plus fréquents dans les terrains ripariens humides, et la "plaine" sur des sols pauvres et plutôt acides. On les trouve tous les deux, avec l'érable argenté (voir Tableau VI), en des formations très homogènes sur les terres inondées au printemps (Fig. 1D[4]).

Indice 2

Les espèces qui portent l'indice 2 (Tableau VI) constituent une catégorie assez hétérogène. Les diverses formules ont en commun ceci: qu'elles ne contiennent qu'un seul facteur primaire. Les formules expliquent suffisamment les préférences écologiques de chaque espèce: *SHC*, plantes de la forêt canadienne humide; *SHD*, plantes des bois humides (*Aceretum saccharini*?, Fig. 1D[4]); *IMD*, *LMD*, plantes indifférentes ou héliophiles exigeant un sol riche. Il est remarquable qu'aucune espèce dans ce tableau ne dépasse 8%, sauf le *Laportea canadensis*, qu'il faudrait rapprocher des quatre espèces classées sous la formule *SHE* (Tableau IV). Quand on aura des données statistiques sur les bois humides à *Acer saccharinum* et *Ulmus americana* (voir Fig. 1D[4]) les rapports de ces espèces et de celles du Tableau V avec l'érablière seront plus faciles à élucider.

Indice 1

L'indice 1 est donné aux espèces dont la formule contient deux facteurs secondaires (voir Tableau VII). La formule *IHD* indique l'absence de réaction vis-à-vis de la lumière et le besoin d'humidité. Par ailleurs, l'habitat est très variable: le *Carex intumescens* se rencontre dans les bois humides

TABLEAU VII

INDICE 1

ESPÈCES DE DIVERS HABITATS (*D*) HUMIDES (*H*) ET LE PLUS SOUVENT OUVERTS

Forme biologique	Espèce	Formule écologique	Pourcentage de présence	Classe phyto-sociologique
H	*Viola pallens*	*IHD*	9	I
H	*Carex intumescens*	*IHD*	7	I
H	*Viola blanda*	*IHD*	3	I
H	*Glyceria striata*	*IHD*	2	I
H	*Carex gynandra*	*IHD*	2	I
H	*Carex brunnescens*	*IHD*	1	I
H	*Galium asprellum*	*IHD*	1	I
H	*Ranunculus repens*	*IHD*	1	I
H	*Equisetum hyemale*	*IHD*	0.5	0
H	*Juncus macer*	*IHD*	0.5	0
H	*Ranunculus pennsylvanicus*	*IHD*	0.5	0
H	*Heracleum lanatum*	*IHD*	0.5	0
H	*Carex trisperma*	*IHD*	0.5	0
H	*Lycopus uniflorus*	*IHD*	0	0
H	*Carex lupulina*	*IHD*	0	0
H	*Carex crinita*	*IHD*	0	0
G	*Osmunda regalis*	*IHD*	2	I
G	*Dryopteris cristata*	*IHD*	0.5	0

et dans les tourbières; l'*Heracleum lanatum* fréquente les fossés et les ruisseaux sous bois; l'*Osmunda regalis* est souvent au bord des lacs, parfois complètement sous bois.

Indice (+)

L'indice (+), Tableau VIII, appartient aux espèces qui ne possèdent qu'un seul facteur secondaire. Les formules *IAD* et *IAU* se rapportent à

TABLEAU VIII

INDICE (+)

ESPÈCES HÉLIOPHILES (*H*) OU INDIFFÉRENTES (*I*) DE TERRAINS TRÈS PAUVRES (*AU*) OU TRÈS HUMIDES (*H*), LE PLUS SOUVENT ACIDES, CARACTÉRISTIQUES DE L'IMMATURITÉ OU DE LA DÉGRADATION NATURELLE DE L'ÉRABLIÈRE

Forme biologique	Espèce	Formule écologique	Pourcentage de présence	Classe phyto-sociologique
M	*Thuja occidentalis*	*IAD*	11	II
M	*Pinus strobus*	*IAD*	7	I
N	*Viburnum acerifolium*	*IAD*	2	I
Ch	*Vaccinium canadense*	*IAD*	2	I
H	*Polypodium virginianum*	*IAD*	3	I
H	*Sanicula marilandica*	*IAD*	2	I
H	*Agrimonia gryposepala*	*IAD*	3	I
H	*Danthonia spicata*	*IAD*	1	I
H	*Oryzopsis pungens*	*IAD*	1	I
H	*Hieracium scabrum*	*IAD*	1	I
H	*Equisetum sylvaticum*	*IAD*	1	I
M	*Fraxinus pennsylvanica*	*LHD*	4	I
M	*Fraxinus nigra*	*LHD*	1	I
M	*Populus balsamifera*	*LHD*	0.5	0
N	*Ilex verticillata*	*LHD*	1	I
N	*Salix* sp.	*LHD*	0.5	0
H	*Thalictrum polygamum*	*LHD*	4	I
H	*Geum rivale*	*LHD*	2	I
H	*Ranunculus sceleratus*	*LHD*	1	I
H	*Polygonum lapathifolium*	*LHD*	0.5	0
H	*Iris versicolor*	*LHD*	0.5	0
H	*Acorus calamus*	*LHD*	0.5	0
H	*Geum strictum*	*LHD*	0.5	0
H	*Glyceria pallida*	*LHD*	0.5	0
H	*Carex aurea*	*LHD*	0.5	0
H	*Decodon verticillatus*	*LHD*	0.5	0
H	*Steironema ciliatum*	*LHD*	0.5	0
H	*Bidens frondosa*	*LHD*	0.5	0
H	*Desmodium canadense*	*LHD*	0.5	0
H	*Anemone riparia*	*LHD*	0	0
H	*Urtica* sp.	*IAU*	0	0
H	*Carex scoparia*	*IAU*	0.5	0
Th	**Satureja acinos*	*IAU*	0.5	0

* *Naturalisée.*

des espèces des terres pauvres et même souvent sèches, en tout cas acides. Les caractéristiques de la pinède s'y trouvent: *Pinus strobus*, *Viburnum acerifolium*, *Danthonia spicata* (Fig. 1D²), de même que le cèdre *Thuja occidentalis* (Fig. 1*D*¹). La formule *LHD* réunit surtout des plantes du rivage. Une seule espèce ici est franchement aquatique, l'*Acorus Calamus*. Les autres se tiennent dans des terrains saturés d'eau, comme le *Bidens frondosa*, le *Geum rivale*, le *Decodon verticillatus*, ou bien font partie d'une association riparienne psammophile, où dominent le *Populus balsamifera*, les saules, le *Desmodium canadense* (voir Fig. 1D⁵), ou encore plongent leurs racines dans les berges riches des fossés, comme le frêne noir, le frêne rouge, et le *Thalictrum polygamum*.

Indice (.)

Le Tableau IX contient les espèces les plus indiscutablement liées à la dégradation artificielle de l'érablière. Les formules *LAD* et *LAU*, en effet, ne contiennent que des facteurs négatifs, aucun facteur primaire ni secondaire. Les espèces de la première série (*LAD*) appartiennent à des associations plus ou moins définies: les *Populus tremuloides*, *Betula papyrifera*, *Vaccinium*

TABLEAU IX

INDICE (.)

ESPÈCES HÉLIOPHILES (*L*) DES LIEUX OUVERTS, POUR LA PLUPART TRÈS ACIDOPHILES, À VALEUR STRICTEMENT NÉGATIVE POUR L'ÉRABLIÈRE OÙ ELLES MARQUENT UNE DÉGRADATION ARTIFICIELLE CERTAINE

Forme biologique	Espèce	Formule écologique	Pourcentage de présence	Classe phyto-sociologique
M	*Betula papyrifera*	*LAD*	8	I
M	*Populus grandidentata*	*LAD*	7	I
M	*Populus tremuloides*	*LAD*	4	I
M	*Betula populifolia*	*LAD*	1	I
N	*Prunus virginiana*	*LAD*	21	III
N	*Prunus pennsylvanica*	*LAD*	16	II
N	*Amelanchier* sp.	*LAD*	3	I
N	*Crataegus* sp.	*LAD*	3	I
N	*Prunus nigra*	*LAD*	1	I
N	*Cornus rugosa*	*LAD*	1	I
N	*Amelanchier canadensis*	*LAD*	0.5	0
N	*Amelanchier laevis*	*LAD*	0.5	0
N	*Rhus typhina*	*LAD*	0.5	0
Ch	*Rhus toxicodendron*	*LAD*	2	I
Ch	*Diervilla Lonicera*	*LAD*	1	I
Ch	*Vaccinium pennsylvanicum*	*LAD*	1	I
Ch	*Spiraea latifolia*	*LAD*	0.5	0
Ch	*Spiraea tomentosa*	*LAD*	0.5	0
Ch	*Rubus allegheniensis*	*LAD*	0.5	0
H	*Fragaria virginiana*	*LAD*	8	I
H	*Fragaria americana*	*LAD*	4	I
H	*Aster cordifolius*	*LAD*	5	I
H	*Anaphalis margaritacea*	*LAD*	3	I
H	*Anemone virginiana*	*LAD*	2	I
H	*Carex communis*	*LAD*	1	I

TABLEAU IX—*fin*

INDICE (.)

ESPÈCES HÉLIOPHILES (*L*) DES LIEUX OUVERTS, POUR LA PLUPART TRÈS ACIDOPHILES, À VALEUR STRICTEMENT NÉGATIVE POUR L'ÉRABLIÈRE OÙ ELLES MARQUENT UNE DÉGRADATION ARTIFICIELLE CERTAINE—*fin*

Forme biologique	Espèce	Formule écologique	Pourcentage de présence	Classe phyto-sociologique
H	*Anemone canadensis*	*LAD*	1	I
H	**Achillaea Millefolium*	*LAD*	3	I
H	*Lobelia inflata*	*LAD*	1	I
H	**Verbascum Thapsus*	*LAD*	1	I
H	*Aster paniculatus*	*LAD*	0.5	0
H	*Aster nemoralis*	*LAD*	0.5	0
H	*Aster puniceus*	*LAD*	0.5	0
H	**Poa pratensis*	*LAD*	0.5	0
H	*Helianthus* sp.	*LAD*	0.5	0
H	*Aquilegia canadensis*	*LAD*	0.5	0
H	*Hypericum* sp.	*LAD*	0.5	0
H	*Epilobium angustifolium*	*LAD*	0.5	0
G	*Pteridium latiusculum*	*LAD*	8	I
G	*Dennstaedtia punctilobula*	*LAD*	2	I
Th	*Gnaphalium sylvaticum*	*LAD*	1	I
N	*Sambucus canadensis*	*LAU*	2	I
Ch	*Rubus idaeus*	*LAU*	7	I
Ch	**Berberis vulgaris*	*LAU*	0.5	0
H	**Prunella vulgaris*	*LAU*	3	I
H	**Polygonum Convolvulus*	*LAU*	3	I
H	*Solidago canadensis*	*LAU*	2	I
H	*Antennaria neglecta*	*LAU*	2	I
H	**Galeopsis Tetrahit*	*LAU*	2	I
H	*Apocynum androsaemifolium*	*LAU*	2	I
H	*Erigeron philadelphicus*	*LAU*	2	I
H	*Chelidonium majus*	*LAU*	2	I
H	*Solidago rugosa*	*LAU*	1	I
H	**Arctium Lappa*	*LAU*	1	I
H	**Antennaria neodioica*	*LAU*	1	I
H	*Leontodon autumnale*	*LAU*	0.5	0
H	**Hieracium aurantiacum*	*LAU*	0.5	0
H	**Hieracium Pilosella*	*LAU*	0.5	0
H	**Taraxacum officinale*	*LAU*	0.5	I
H	**Leonurus Cardiaca*	*LAU*	0.5	0
H	**Rumex acetosa*	*LAU*	0.5	0
H	**Silene cucubalus*	*LAU*	0.5	0
H	**Stellaria media*	*LAU*	0.5	0
H	**Stellaria longifolia*	*LAU*	0.5	0
H	*Trifolium repens*	*LAU*	0.5	0
H	**Nepeta Cataria*	*LAU*	0.5	0
H	**Ranunculus acris*	*LAU*	0.5	0
H	**Conringia orientalis*	*LAU*	0.5	0
H	**Solanum Dulcamara*	*LAU*	0.5	0
H	**Polygonum Persicaria*	*LAU*	0	0
Th	**Geranium Robertianum*	*LAU*	3	I

* *Naturalisée.*

pennsylvanicum, *Aster nemoralis*, *Epilobium angustifolium* sont caractéristiques du *Betuletum* qui colonise la forêt coupée. Les *Amelanchier*, les *Crataegus*, et les *Prunus*, les *Fragaria*, le *Verbascum Thapsus* caractérisent le climax secondaire que constituent les pâturages. Tandis que les espèces correspondant à la formule *LAU* sont des mauvaises herbes, habiles à s'insinuer partout, toujours agressives et ordinairement grégaires: tous les sols leur sont bons et toutes les expositions (mais surtout le plein soleil). La plupart de ces dernières sont introduites.

Classification des relevés

La répartition qui précède, et qui situe chaque espèce dans une classe écologique par rapport à sa valeur constructive pour l'association qui nous intéresse, est basée sur l'écologie totale de chaque espèce. Elle ne prétend pas reconnaître la valeur intrinsèque, les virtualités de chaque espèce, mais plutôt l'expression permise à ces virtualités dans le milieu naturel. Ainsi, l'on sait fort bien que l'érable argenté est très résistant à la sécheresse, mais il ne résiste apparemment pas à la concurrence dans les milieux secs, puisqu'on le trouve infailliblement dans les lieux humides à l'état spontané. Une foule d'espèces mésophiles, de même, survivraient facilement dans un sol moins riche n'était la concurrence des rudérales agressives. Il n'est donc pas tenu compte ici des exigences fondamentales des espèces—qui nous sont inconnues dans la plupart des cas, l'expérimentation pouvant seule les révéler—mais de leur comportement usuel. Il est d'ailleurs évident que ce comportement constitue un bien meilleur indice que des virtualités tenues en échec par le milieu.

La valeur d'indice de chaque espèce ayant donc été déterminée, il devient possible d'élaborer une échelle de pointage qui nous permettra de classifier les relevés selon leur degré de pureté. Ce sont ces relevés sélectionnés qui serviront de base au tableau définitif de l'*Aceretum saccharophori*.

Remerciements

Ces recherches ont été entreprises au Jardin botanique de Montréal grâce à deux octrois (1940 et 1941) du Conseil national de Recherches que je tiens à remercier vivement. Je me dois de rendre hommage aussi à mon maître, le professeur J. Braun-Blanquet, de Montpellier qui fut mon initiateur à la phytosociologie et au R. F. Marie-Victorin qui a bien voulu reviser le manuscrit et m'offrir de très utiles suggestions. Je remercie également M. André Lafond qui m'a accompagné sur le terrain et a assumé toute la partie matérielle du travail ainsi que MM. Ernest Rouleau, Auray Blain, et James Kucyniak.

Summary

The area of the sugar maple grove occupies, roughly, the northern half of the Northeast-American deciduous forest, bounded on the east by the Atlantic, the south by the subtropical sclerophyllous woodland, the west by the prairie,

and the north by the Canadian spruce forest. The area studied here is shown by broken lines in Fig. 6 and corresponds to a fairly homogeneous geographical unit. Table I affords a comparison with similar maple formations elsewhere (Indiana, Michigan, Northern Ontario) and tends to demonstrate that similarities are strong enough to justify the conception of a single large unit (*Aceretum saccharophori*) although dissimilarities indicate a large measure of geographical phytosociological segregation.

An attempt has been made to follow no preconceived pattern to define the sugar maple grove, but to survey indifferently stations where the sugar maple (*Acer saccharophorum*) was present. Thus 180 stands were examined and carefully studied as to soil, height, and diameter of trees, exposure, slope, percentage of cover of different strata and complete list of all species present with abundance and sociability category, the latter according to Braun-Blanquet (1).

These 180 stands, in which 346 species occurred, proved to be of very unequal value: some were visibly in an advanced stage of degradation either through lumbering, cutting, burning, pasturing, or sugaring; some were in eccentric positions as regards drainage or altitude or some other local condition. It therefore seemed advisable to sort out the individual reports according to their "degree of purity" in order to devise an appreciation scale based on the factors known to determine the ideal conditions of the maple grove as distinguished from other formations in the same area (Fig. 1) and from its own forms of natural or artificial degradation.

It has seemed logical first of all, therefore, to determine the index value of the 346 species, since they are the determining sociological element. Of course, some are plastic and some are rather narrowly limited by one particular factor. The latter are naturally the best indicators. Five principal points are of interest for each species.

1. The life-form (10), particularly significant in an association submitted to such extreme seasonal variations in its microclimate (see Fig. 2), and the biological spectrum (Table II).
2. The percentage of presence in the 180 stands.
3. Reaction to light, the maple grove being characteristically a sciophilous habitat.
4. Reaction to humidity, mesophily being the rule in the maple grove.
5. Fidelity to the maple grove.

The following considerations demonstrate quite clearly the heterogeneous nature of the material analysed:

1. Life-forms do not rank very close to the European beech wood (Table II), an analogous association (although other explanations are available, especially as concerns the phanerophytes).
2. Percentage of presence (Fig. 2) shows an overwhelmingly large number of ecologically indifferent species, as compared with an homogenous sampling in a regularly described association (Fig. 3).

3. Shade-loving plants, although numerous (Fig. 4) are accompanied by a very large number of indifferent or frankly heliophilous species.
4. Mesophilous species are most numerous also (Fig. 5), but the number of hygrophilous and drought-resisting species is quite considerable.
5. Species practically not found outside the maple grove are in quite sufficient number: all the characteristics are there and many more, ecologically unimportant; the species introduced accidentally from other formations (see Fig. 1) may be numerous, but it is their abundance in individuals that counts, not their variety.

Therefore, an index value has been attributed to each species, due consideration being given to the above-mentioned factors. Thereby, typical stands will be isolated and they alone should serve to establish the association chart and biological formula of *Aceretum saccharophori*.

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GROWTH OF THE SALMON EMBRYO[1]

By F. R. Hayes[2] and F. H. Armstrong[3]

Abstract

Wet and dry weights of Atlantic salmon are given up to the end of yolk sac absorption, and from them the growth rates are determined. Attempts are made to smooth the growth curve by the methods of Brody, Murray-Schmalhausen, and MacDowell *et al.* Of these the last is best taking zero time as nine days after fertilization. It is concluded that, as to weight, the interval considered ends before the point of inflection of a Sachs growth cycle. Growth in length, however, represents a complete cycle, hence there can be no simple quantitative relation between length and weight. Deviations from the smoothly descending relative growth rate (RGR or Minot) curve are considered, with the conclusion that all such irregularities so far presented can be attributed to random errors (except possibly the posthatching rise in RGR of the trout at 12° reported by Wood). In general weighing is not sufficiently sensitive as a method, to permit a detailed description of the RGR.

The purpose of this paper is to interpret a series of weights of developing embryos of the Atlantic salmon, *Salmo salar* L., taken from as soon after fertilization as possible up to the time of complete absorption of the yolk sac. Groups of 10 embryos, dissected off the yolk sac, were placed in tared Pregl micro weighing bottles and weighed to the nearest 0.2 mg. to obtain the "wet weight"; they were then dried at 100° C. to a constant value called the "dry weight". Five to 10 such groups were used in order to obtain each of the figures given in Table I, Columns 3 and 4—thus each value is based on 50 to 100 embryos. In all about 2000 embryos were used. Further details of technique, including the use of formalin for fixation of early stages, are given elsewhere (9).

It will be convenient to examine the salmon values in relation to the classical ideas of growth, and this will be facilitated by a brief preliminary description of a generalized growth cycle and the chief curves derived from it. Consideration will also be given to some of the formulae that have been put forward for the purpose of smoothing embryonic growth curves.

A Growth Cycle and Its Derivatives

If one measures the weight or length of a growing organism at various intervals of time, any two determinations differ by amounts somehow related

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to the time that has elapsed between them. If time is plotted on the abscissa and weight or length on the ordinate the resultant curve is often more or less S-shaped (Fig. 1A). Sachs (22) called the data described by the curve, a growth cycle or great period of growth. Such a curve begins at or near the zero point and is at first convex to the abscissa, later concave, so that somewhere in the middle there must be an inflection or change of direction of

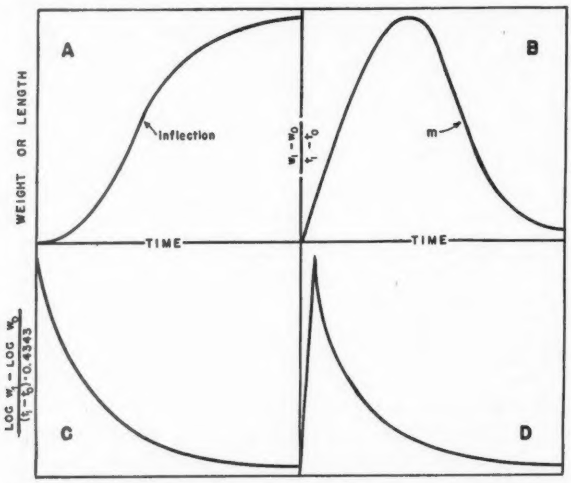

FIG. 1. *A growth cycle and its derivatives. A. Complete cycle of Sachs. B. Absolute growth rate. C. Usual relative growth rate or Minot curve. D. Occasional RGR as in a few plants.*

curvature. The curve is characteristically asymptotic to the final size, i.e. it never really becomes flat at the top, which means in theory that an organism never stops growing, although up at the top of the S the rate of increase is so small that the slope ceases to be of interest. Although a growth cycle, mathematically, extends to infinity, in practice there is often a more or less clearly marked end, e.g. the onset of a second cycle or the withering of a plant; it is with reference to such an end that expressions like "centre of a cycle" are used in the following pages.

Growth cycles may be observed when the environmental conditions are kept approximately constant, as in Sachs' classical experiment on the increase in length of the bean during a few weeks in summer. They may also be observed, in spite of fluctuating conditions, when the unit of measurement is the year, for under such circumstances seasonal variations cancel themselves out, e.g. Pütter's observations on length growth of the herring, as cited by Backman (2). On the other hand no S-shaped curve would be expected, for example, in the growth of an apple bud, which begins in one summer, is suppressed during the winter, and goes on in the spring to become a blossom or leaf. The same is true of the discontinuous development of insect larvae.

Moreover there can be no general growth cycle for a species in which the individuals differ in some essential habit; for example the Atlantic salmon may go to sea in its second or third year, return in its fourth or some later year, and may or may not return to the river a second or third time.

Some of the properties implicit in an *S*-curve can be brought into view by changing it around to show absolute growth rate (or AGR) (Fig. 1B), which answers the question "How much is added per unit time to what is already there?" The AGR is obtained by dividing the increase in weight by the increase in time, or

$$AGR = \frac{dw}{dt} = \frac{w_1 - w_0}{t_1 - t_0}$$

approximately, where w_0 is the weight at any time, t_0, and w_1 is the weight at a slightly later time, t_1. The curve passes through a maximum or peak, to the right of which there is an inflection, *m*. The presence of *m* is a mathematical necessity. It is mathematically possible, but not necessary, for a second inflection to occur to the left of the peak, more or less opposite to *m*. (But data that can be reduced to a straight line by the method of MacDowell *et al.* described below, cannot exhibit any second inflection in the AGR curve.) The AGR curve should begin at the origin, i.e. have a zero value at zero time. Unfortunately biological zero time is difficult to determine, being reckoned sometimes from fertilization, sometimes from the first formation of the embryonic axis, and sometimes from a mathematically convenient point without biological meaning. Thus the theoretical requirement is not always realized.

In 1891 Minot suggested that the growth rate should be expressed in terms of the material already there by use of the formula:

$$\text{Percentage growth rate (Minot)} = \frac{100\ (w_1 - w_0)}{w_0\ (t_1 - t_0)}.$$

Schmalhausen (23) and Brody (4) have independently shown that the Minot formula tends to give results that are too high, especially in the youngest stages, and have proposed to substitute for it

$$\text{Relative growth rate} = \frac{C_v}{\text{(Schmalhausen)}} = \frac{k_1}{\text{(Brody)}} = \frac{dw}{w.dt} = \frac{\log w_1 - \log w_0}{(t_1 - t_0).0.4343}.$$

C_v (or Brody's k_1) has been used for the calculations of relative growth rate in Table I. It is a better version of $\frac{\text{Minot}}{100}$. ("Log" throughout this paper refers to common logarithms to the base 10.)

Fig. 1, C and D shows typical relative growth rate or Minot curves. In a few plants the curve may have the same form and properties as the absolute growth rate curve, but the peak is far to the left (Fig. 1D). An example is found in Silberschmidt's work, cited by Backman (2, p. 925), on the growth of the oat at 4° C. Such curves are special cases, for in nearly all plants, and in all animals so far investigated (except for Privolniev's (19) salmon

TABLE I

WEIGHTS ARE OF ONE EMBRYO IN MILLIGRAMS. TO OBTAIN COLUMN 5 EACH WEIGHT READING IN COLUMN 4 WAS AVERAGED WITH THOSE BEFORE AND AFTER IT. THE SAME WAS DONE WITH COLUMN 2 TO OBTAIN THE TIMES GIVEN IN COLUMN 7

1	2	3	4	5	6	7
Days before and after hatching	Days after fertilization	Dry weight	Wet weight	Averaged wet weight	Log Col. 5	Averaged days for Col. 5
−40	10		.16	.16	.2041	10
−39	11		.31	.31	.4914	11
−38	12		.45	.65	.8129	12
−36	14	.19	1.2	1.1	.0414	14
−33	17	.25	1.6	1.7	.2304	17
−31	19	.35	2.2	3.2	.5051	20
−26	24	.5	5.8	5.3	.7243	23
−23	27	.8	7.8	7.7	.8865	27
−19	31	.9	9.4	9.1	.9590	30
−18	32	1.0	10.2	10.6	.0253	32
−17	33	1.3	12.3	11.8	.0719	34
−14	36	1.5	13.0	14.2	.1523	37
− 9	41	2.0	17.4	16.8	.2253	41
− 3	47	2.4	20.0	20.0	.3010	45
− 2	48	3.1	22.6	22.8	.3579	49
3	53	3.4	25.8	25.3	.4031	53
7	57	3.8	27.5	30.5	.4843	60
19	69	5.8	38.2	37.4	.5729	67
26	76	7.4	46.5	44.3	.6464	75
30	80	7.7	48.1	48.9	.6893	80
33	83	8.3	52.2	52.7	.7218	84
38	88	9.1	57.7	61.3	.7875	89
47	97	12.8	73.9	77.1	.8871	101
68	118		99.6	99.6	.9983	118

8	9	10	11
Central dates from Col. 7	Absolute growth rate from Cols. 5 and 7	C_v or relative growth rate from Cols. 6 and 7	$C_t\,(t-9)$ from Cols. 8 and 10
10.5	.15	.66	1.0
11.5	.34	.74	1.8
13.0	.23	.26	1.1
15.5	.20	.15	1.0
18.5	.50	.21	2.0
21.5	.70	.17	2.1
25.0	.60	.094	1.5
28.5	.47	.056	1.1
31.0	.75	.076	1.7
33.0	.60	.054	1.3
35.5	.80	.062	1.6
39.0	.65	.042	1.3
43.0	.80	.044	1.5
47.0	.70	.033	1.3
51.0	.62	.026	1.1
56.5	.74	.027	1.3
63.5	.99	.029	1.6
71.0	.86	.021	1.3
77.5	.92	.020	1.4
82.0	.95	.019	1.4
86.5	1.7	.030	2.3
95.0	1.3	.019	1.6
109.5	1.3	.015	1.5

embryo values discussed below), the curve starts at a maximum and falls continuously, approaching the time axis asymptotically (Fig. 1C). Whether it has bumps on it representing fluctuating growth rates, and if so how many, remains an open question.

Irregularities in Growth Rate Curves

It is true of growth rate curves more than any other under consideration, that there have to be many closely spaced observations for an accurate representation of the facts. As Figs. 3 and 6A show, the points fluctuate a good deal, thereby increasing the difficulty of smoothing the curve by eye.

The cause lies in the arithmetic, for it will be noticed in the absolute growth rate (and the same reasoning would apply to the relative growth rate),

$$AGR = \frac{\text{large weight minus slightly smaller weight}}{\text{large time minus slightly smaller time}} .$$

There are two chief sources of error. First, the numerator shows errors in weight estimations, which are relatively greater in younger stages when the embryos are very small; second, errors arise from the fact that even under identical conditions development does not proceed for all embryos at the same rate, which is equivalent to an error in the times given in the denominator. The latter may be relatively unchanged throughout development. If hatching, for instance, were to be placed at a certain date plus or minus one week, the end of yolk absorption might be taken at plus or minus two weeks or more. To illustrate specifically, taking letters to represent the relative errors,

$$AGR = \frac{(22.8 \pm p) - (20.0 \pm q)}{(49 \pm r) - (45 \pm s)}$$

$$= \frac{2.8 \pm (p + q)}{4 \pm (r + s)} .$$

This is approximately

$$AGR = 0.7 \times [1 \pm (8.1p + 7.1q + 12.3r + 11.3s)\ ].$$

It is obvious that the calculation of a growth rate causes figures with small errors to be changed into a figure with a much larger error. Some caution is accordingly necessary in the matter of placing a physiological interpretation on the scattering of growth rate points, as Privolniev (19) has done.

The Growth Curve of the Salmon

Fig. 2 shows the wet and dry weights of the salmon embryo plotted against time (Table I, Columns 2, 3, and 4). The ordinates have been selected in such a way as to suggest that the dry weight rises relatively more rapidly than the wet weight, which is true, and which leads to the conclusion that the proportion of water in the embryo begins to decrease some time before hatching and becomes progressively less as development proceeds. Otherwise the curves are similar in form, and when they are compared to Fig. 1A it is immediately apparent that the point of inflection of the latter has not yet been reached by the salmon. Thus the salmon, up to the completion of its yolk sac absorption, represents less than half of a growth cycle. This important conclusion, which differs from that of some other authors, will be referred to again in the next section.

In the remainder of this paper only the wet weight values will be used for plotting curves, for the dry weights would probably add little to the conclusions to be drawn, and are moreover, incomplete at the beginning and end.

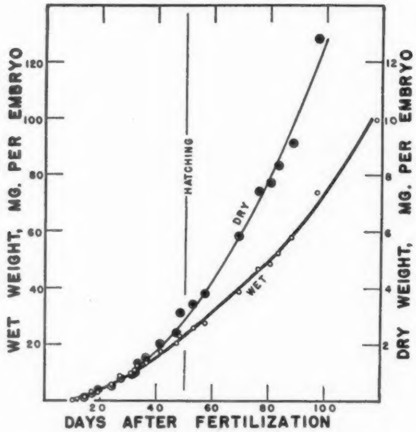

FIG. 2. *Growth of the salmon expressed in wet and dry weight.*

The Absolute Growth Rate

Because of the tendency for points on growth rate curves to fluctuate, it was considered advisable to carry out a preliminary smoothing before plotting the absolute growth rate. Each weight reading, and its corresponding time reading, was averaged with those before and after it, the new results being given in Table I, Columns 5 and 7. From these the AGR was calculated (Table I, Column 9, and Fig. 3). The method of getting Column 9 is equivalent to ignoring the two items of Column 4 nearest to the central date and using only the two items next further away. According to Thompson (26, p. 138) the method was first used by Gauss. Its advantage lies in the clarification of general trends, its disadvantage is a tendency to minimize or obliterate sudden changes which may be real.

If the prehatching part of the AGR curve be projected back to the abscissa it is found that the intersection falls at five days, a value for which no great accuracy can be claimed, and which might precede, or at latest coincide approximately with the formation of the embryonic axis which in the present observations occurred at about nine days. Thus there cannot be, after the embryo is formed, any sweeping concavity in the curve. It is more likely that the embryo starts off at a maximum AGR. However, other workers have reported an early inflection in AGR curves of trout (8 and 13), and salmon (19). Privolniev's early values are completely at variance with the present ones (see below); as to possible differences between the salmon and trout, no decision can be made at present.

An additional peculiarity of the salmon is the interruption of the curve at hatching, which is less unexpected in view of previously noted interruptions of particular embryonic activities by hatching (10). Whether there is

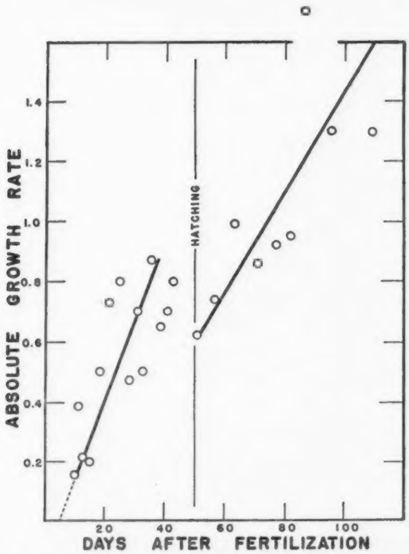

FIG. 3. *Absolute growth rate of the salmon, from wet weights.*

actually a dip in the AGR curve or merely a failure to continue the upward slope, is not certain. The difference in slope between the pre- and post-hatching curves is not significant. It may be doubted whether the hatching interruption occurs under all conditions, or whether there is not perhaps an optimum temperature at which development proceeds through hatching without a break, but above and below which hatching exercises an interfering action.

A third feature of the salmon curve (noted in the preceding section) is that the peak, as in Fig. 1B, has not yet been reached, from which it is concluded that the first winter of salmon life cannot be called a growth cycle in the sense of Sachs. Working on the trout, Wood (30) also failed to find a decline in AGR. This is not to deny that when the yolk is all gone, or nearly all gone, the embryo, owing to starvation, will necessarily stop growing. Gray (8) and Kronfeld and Scheminzky (13) reported for the trout and Privolniev (19) for the salmon that a decline in AGR begins before the yolk is quite gone. Differences may be in part due to the difficulty in deciding when the yolk is entirely used up, for there is still some left when the external sac has disappeared. If the reported decline in AGR could be abolished by feeding, the idea of a growth cycle would have to be abandoned; the experiment has been done with trout by Willer (29). He weighed whole larvae, hence his values represent embryo gain minus yolk loss, which would tend, if anything, to produce the effect of a decline after hatching even if none existed

for the embryo. Feeding was begun, in conformity to hatchery practice, when the yolk sac was partly absorbed, and there was in fact no sign of a decline in growth up to the time the fry were ready for planting, two months after the yolk sac had completely disappeared.

Smoothing the Salmon Curve

A simple and somewhat primitive method of smoothing the wet weight curve has already been described. Various workers have recommended other methods involving the use of algebraic expressions, some of which must be considered. It will not however, be possible to deal with formulae having the purpose of describing the whole *S*-curve, as in Fig. 1A, because the salmon does not, during the first winter of life, reach the point of inflection. Therefore knowledge is lacking as to the final weight attained and the total time for a cycle, which are required for the application of equations such as those of Robertson (21) and von Hoesslin (12). An objection to other of these formulae is that most of them have three arbitrary constants, being of the general form:

$$\log w = k_0 + k_1 (t) + k_2 (t)$$

where k_0 is the intercept, k_1 the slope, and k_2 the correction for the slope; (t) may mean variously $\log t$, t^2, $\log {}^2t$, etc. (3). It is extremely doubtful whether there are any embryonic weight data precise enough to warrant for their description the use of three arbitrary constants. Hence, the salmon weights cannot be profitably interpreted in terms of such expressions.

An alternative method of treatment, more desirable for present purposes, is to deal only with the part of a Sachs curve in which one is interested. The curve readily divides itself into two, or sometimes three parts (when the middle segment appears as a straight line). Of these only the first part, which is convex to the abscissa, parallels the salmon weight results. To expressions describing it the objection has been raised that they do not give reasonable results when the curves are projected either to zero time or to infinity, or both. Thus an embryo might, according to the formula, grow to infinite size. As it is not proposed to extrapolate the salmon results the objection need not be taken seriously. The purpose of curve smoothing is to force the graph into a straight line in order to permit easy interpolation.

The first expression to be considered is that of Brody (4). In working with embryonic chicks Brody was struck by the fact that when the log of the weight was plotted against time a series of straight lines resulted, and this led him to the view that the relative growth rate, k_1, remained constant for a time, then changed suddenly. During one of these constant periods the rate could be represented by the expression

$$\log w = k_0 + k_1 t.$$

When the slope changed there were new values for k_0 and k_1. Brody pays no attention to the k_0 or intercept values, which are wholly unreasonable, but is concerned entirely with the slope, k_1. In the upper part of Fig. 4,

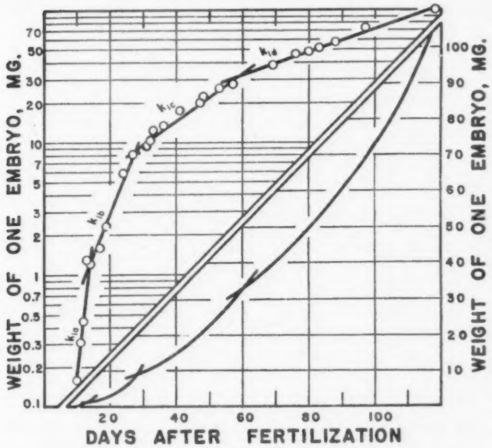

FIG. 4. *Upper part, salmon wet weights as smoothed by Brody's method in which weight is plotted on a logarithmic scale, time on an arithmetic scale. Lower part, a Brody interpretation of Fig. 2.*

by plotting the wet weights on a logarithmic scale, an attempt has been made to apply Brody's method to the salmon. In accordance with Brody's procedure the breaks have been selected arbitrarily. It has been possible to show by Fisher's method of analysis of variance, that the slopes of the lines differ significantly from each other. Except for the second segment, k_{1b}, it has not been possible to show with existing data, that the segments between the breaks are well fitted by straight lines. Additional ground for scepticism is provided by the lower part of the figure, which represents the original growth curve as smoothed from the Brody results. Considerably more evidence than is available would be required before the lower part of Fig. 4 could be accepted as a description of the data set down in Fig. 2. Nevertheless whatever may be the quantitative difficulties with Brody's method of presentation, it does direct attention to the idea that the growth rate may change abruptly.

While Brody considered the relative growth rate as changing at intervals from one constant value to another constant value, Friedenthal (6) and Murray (17) had, with similar data, come to a somewhat different conclusion, namely that when embryo weight is plotted against time on logarithmic paper (where the abscissa and ordinate are proportional to the logs of the numbers), the result is a straight line;

$$\log w = k_0 + k_1 \log t.$$

This is another way of saying that the corners of the segments in Brody's curve (lower part of Fig. 4) should be rounded off, and the whole represented

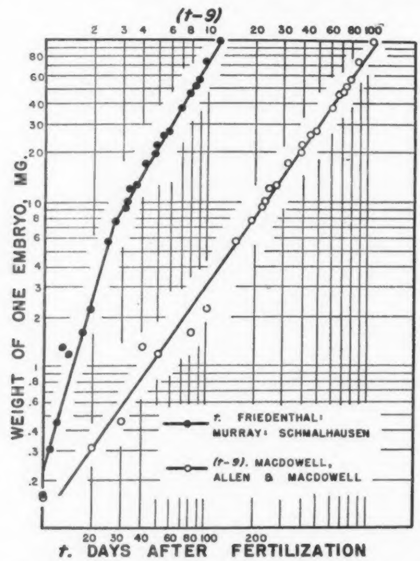

FIG. 5. *Data of Fig. 2 as changed by plotting on logarithmic paper. Left, when fertilization is taken as zero time. Right, when the formation of the embryo at nine days is taken as zero time.*

as a generalized parabola of the type $y = Ax^{k_1}$. Schmalhausen, although he started out from an entirely different point of view, arrived at the same conclusion (24). In Fig. 5 the Friedenthal-Murray-Schmalhausen equation is tested by a plot of the salmon data on logarithmic paper. It is apparent that the values cannot be fitted by one straight line, although they can be fitted by two straight lines with a break that corresponds to that between segments two and three of the Brody curve. (Note: Glaser's (7) modification of the above formula offers no improvement when applied to the salmon data.)

The final step in curve smoothing was taken by MacDowell, Allen, and MacDowell (15) who proposed to write $(t - n)$ instead of t in the preceding formula, where n is the number of days after fertilization at which the embryonic axis is established. In the present case n may be taken with fair probability as 9. The theory is that before n days when there is an undifferentiated mass of cells spreading over the yolk sac the rules of growth will not be the same as later, when the observer is dealing with the embryo proper. Hence time should be reckoned from the establishment of the permanent plan. While n is of course a new constant, it is a natural one, directly observable in the material, to whose use no objection can be taken. In Fig. 5, $(t - 9)$ has been plotted against w on logarithmic paper, as a test of the formula

$$\log w = k_0 + k_1 \log (t - 9).$$

The points can be fitted by one straight line, which means that the salmon

data have been smoothed in a systematic way according to a very simple plan. The MacDowell formula has been successfully applied, by proper choice of n to a considerable variety of embryonic data. The time before n is necessarily considered as irrelevant, for trouble would arise if log $(t - n)$ were applied when t is less than n, as negative numbers do not have real logs.

Brody's formula directs attention to sudden change; MacDowell's formula suppresses evidence of sudden change. The views are not inconsistent, any more than a description of the earth as round contradicts knowledge of mountain heights and ocean depths. On the causes of irregular variation in salmon growth rate, if such exist, the evidence is still inadequate. But even where full details are available about the extent and nature of a fluctuating growth rate, those who prefer a single, comprehensive formula are willing to apply it to the results. Thus Courtis (5) finds that the growth of the City of Detroit can be treated as a Sachs cycle and fitted by the three-constant formula of Gompertz, with an average deviation of only 5% of the mean "omitting the ten depression years: 1830 and 1834 following the War of 1812; 1860, 1864, and 1870, the Civil War depression: and 1930, 1932, 1934, 1935, 1936, the World War depression years. The A. D. for these years was 38%. Three other large errors occurred between 1840 and 1850."

The Relative or Percentage Growth Rate

If C_v be plotted against time, a Minot curve should result, although the latitude of interpretation discussed in the preceding section will have a corresponding effect on its shape. It is well to begin with a comparatively unsmoothed curve, Fig. 6A, which was constructed from Table I, Column 10. The irregularities in the present salmon values appear to be random, and provide no evidence of systematic deviation from a smoothly descending curve. In fact the curve is like that for warm-blooded vertebrate embryos (18), and does not justify the view that fish embryos differ in their growth mechanism from birds and mammals.

Conformation of the similarity is provided by the values in Table I, Column 11, for according to Schmalhausen's "law of growth" (24) the product of the multiplication of the relative growth rate by the age is a constant,

$$C_v t = K.$$

This is just another way of saying that log weight plotted against log time gives a straight line (MacDowell *et al.* curve). Schmalhausen's table (reproduced in 18, p. 436) shows that for warm-blooded animals the constant is usually between three and four. The only fish embryo included is the trout for which $C_v t = 2.06$ (data of Kronfeld and Scheminzky). Time is reckoned from the establishment of the embryonic axis, 10 days in the trout. Under present conditions time is taken as $(t - 9)$, and on the average of Table I, Column 11,

$$C_v\,(t - 9) = 1.47 \pm 0.05.$$

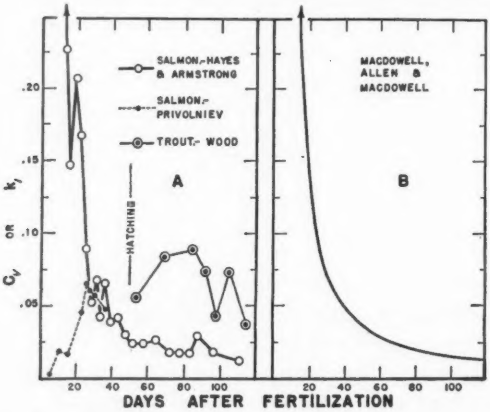

FIG. 6. *Relative growth rate of the salmon. A, main curve from Table I, Column 10; lower left from Privolniev's (19) salmon dry weights; right from Wood's (30) wet weights of trout reared at 12° C., with a time correction to make them fall above the corresponding salmon stages. B, smoothed by the method of MacDowell et al. (15), see Fig. 5.*

The important thing is not the magnitude of 1.47 which could be altered at will by changing the temperature, but the existence of a constant at all, suggesting as it does that the growth curve (Fig. 2) is of parabolic type.

The foregoing paragraphs are at variance with the conclusions to be drawn from Privolniev's (19) set of salmon dry weights. The chief difference lies in Privolniev's early C_v values, reproduced in Fig. 6A, showing the Minot curve rising at the start instead of falling. Privolniev's first values (for 35 embryos) were: three days, 17.3 mg.; nine days, 18.0 mg.; 17 days, 21.7 mg. Thus in the first three days the embryo must have grown nearly 17.3 mg., in the next six days only 0.7 mg. Moreover, it is stated that the formation of the embryo occurred at 11 days, or after the first two weighings, so that the latter must have included additional material. The rest of Privolniev's curve (not illustrated here) falls like the present one except for an interval after hatching when there is for a time, an apparent rise of doubtful validity. The rise shows much more clearly in Wood's (30) values, based on trout wet weights at 12°, which are also placed in Fig. 6A. The C_v values are from Wood's original data, but in placing the points on the figure, a time correction has been applied in order to make them fall above the corresponding developmental stages in the salmon.

For the beginning of the curve there are only Privolniev's values and the present ones, but for the interval after hatching there are several. Table II gives an opinion on a survey of these (not necessarily that of the author). The question is whether there is a hump on the Minot curve after hatching (and therefore whether the fish embryo differs from warm-blooded embryos in its habit of growth). The majority answer is certainly negative. If there is, at higher temperatures, as Wood's results suggest, an increase in the

TABLE II

ANSWERS TO THE QUESTION OF WHETHER THE RELATIVE GROWTH RATE, C_v, INCREASES AFTER HATCHING

Observer	Material	Wet wt. or dry wt.	Increased C_v after hatching
Kronfeld and Scheminzky (13)	Trout	Wet	No
Kronfeld and Scheminzky (13)	Trout	Dry	No
Gray (8)	Trout	Wet	No
Wood (30) at 12° C.	Trout	Wet	Yes
Wood (30) at 7° C.	Trout	Wet	Doubtful
Wood (30) at 3° C.	Trout	Wet	No
Privolniev (19)	Salmon	Dry	Doubtful
This work	Salmon	Wet	No

relative growth rate after hatching, it follows that hatching time must correspond to a minimum value. This would fit in with the finding of Hayes and Ross (11, p. 364) who showed that the storage of fat by salmon embryos is interrupted at the time of hatching. Obviously the effects of temperature on the shape of the growth rate curve deserve further investigation.

Fig. 6B shows the RGR as plotted by the method of MacDowell *et al.*, which Schmalhausen himself has come to use in his later papers (25). Fig. 7A gives the RGR according to Brody. The discontinuous nature of the curve

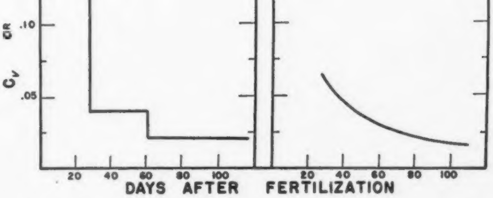

FIG. 7. *Relative growth rate of the salmon. A, calculated from a curve smoothed by the method of Brody (4), see Fig. 4. B, smoothed by the method of Friedenthal-Murray-Schmalhausen, see Fig. 5.*

is apparent and emphasizes again the individuality of Brody's views. Fig. 7B follows the method of Friedenthal-Murray-Schmalhausen, with a break in the centre corresponding to the central break in Brody's curve.

Since the RGR provides a most instructive approach to growth problems it is unfortunate that no unanimity of opinion exists as to the best means of representation. Statistical methods cannot provide the basis for a decision between the possibilities shown in Figs. 6 and 7, and in their absence the following conclusions are suggested:

1. When based on measurements of weight, a single general description of the whole curve is more to be desired than one which breaks it into parts.
2. Hence the modification of MacDowell *et al.* is to be preferred to the original method of Friedenthal-Murray-Schmalhausen.
3. While there may well be variations from time to time in the smooth descent of the RGR, the method of Brody does not provide a conclusive demonstration of them.
4. In view of the errors involved, measurements of weight would appear to lack sufficient sensitivity to serve for a detailed description of the RGR.
5. Progress in detailed description of the RGR is likely to come through a study of the fluctuations in embryonic respiration (20), the varying effect of temperature on differentiation and growth (14, 27, 28), and the times when special reactions such as glycogen synthesis are initiated by the embryo (10).

Growth in Length

Lengths of trout embryos have been measured by Willer (29) under hatchery conditions, with feeding begun at the usual time, and Allen (1) has published a series of such measurements on the salmon, which was not fed. Both find a complete growth cycle, like Fig. 1A, with the inflection, in the growth curve of the salmon, only 10 days after hatching. When length is plotted against time in Allen's curve the portion before the inflection is a straight line so that

$$l = a + bt\,.$$

Nevertheless the MacDowell formula will fit, hence

$$\frac{d \log l}{d \log (t - 9)} = 1\,.$$

With an abrupt change in slope the MacDowell equation also fits approximately the postinflection part of the curve, except for the final points, where growth had practically stopped. The inflection occurs long before the already discussed starvation inflection in weight, which some workers have described (8). Several conclusions may be drawn.

1. There can be no simple mathematical relation between length and weight such as

$$w = l^n$$

as has been suggested by Schmalhausen (23) for a variety of embryos.

2. Formulae such as that put forward by Backman (2) purporting to describe either weight or length curves with equal ease, cannot be used for a description of both processes in the same period of salmonid development. (Backman also uses area as an alternative unit).
3. Growth cycles in the sense of Sachs may be less general than is commonly thought, since a demonstration of their existence in terms of one unit does not constitute evidence about some other unit.

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